Notes on Atlantic and other Asteroidea. 4. Families Poraniidae and Asteropseidae

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Introduction

The skeletal structure of the poraniid starfishes, upon which the classification relies, is hidden or at least obscured by the more or less thickened body wall and opaque skin. X-radiographs of some North Atlantic specimens have thrown new light on the limits of several taxa. The study has been helped by additional material, from various museums and oceanographic institutes, notably from recent collections of the *Discovery,* RSS *Challenger, Walter Herwig* and *Alvin,* as well as many type specimens. Two inter-family transfers of genera are also made: the Southern Ocean genus *Poraniopsis* Perrier—hitherto placed in the Echinasteridae despite its name—is now included in the Poraniidae while conversely *Poraniella* Verrill is transferred from the Poraniidae to the Asteropseidae. In view of previous confusion between these two families, the paper is prefaced by full diagnoses of both. A tabular key for characters of the genera of Poraniidae is appended.

Systematic Account

Family *ASTEROPSEIDAE* Hotchkiss & Clark

Asteropsidae Perrier, 1884: 154.
Gymnasteriidae (pt) Sladen, 1889: 355–356; Perrier, 1894: 327.
Asteropidae Fisher, 1908: 90; 1911 (pt): 247–248; Verrill, 1915: 86.
Poraniidae (pt) Spencer & Wright, 1966: U69.
Asteropseidae Hotchkiss & A. M. Clark, 1976: 266; Blake, 1980: 179; 1981: 381, 391.

A family of the order Valvatida with body form stellate, but the young nearly pentagonal, interradial arcs rounded or sometimes with a blunt angle; arms normally five, flat below, convex or carinate above, there being a distinct ventrolateral angle, entirely covered by more or less thickened skin, opaque and tending to obscure the skeleton in larger specimens, $R > 20$ mm; abactinal skeleton with primary calycinal plates usually distinguishable, small specimens with compact, flat, initially rounded or hexagonal somewhat imbricating plates (as in the Atlantic genus *Poraniella* which is only known at $R < 20$ mm) arranged in longitudinal series but becoming an open reticulum with linking secondary plates, armed with single carinal spines only (*Asteropsis*), spaced fine spines (*Poraniella*), numerous spines (*Valvaster)* or completely spineless (other genera); abactinal papulae single in small specimens but becoming grouped in the skeletal meshes in larger ones; marginal plates well developed, inferomarginals thick wedge shaped, usually projecting to form a ventrolateral angle, variously armed to match the abactinal armament (*Poraniella* with a horizontal fringe of divergent spines along the edge and a few smaller ones above), superomarginals usually bare and more or less inset but with a few small spines in *Poraniella* or with multiple spines and often a conspicuous pedicellaria in *Valvaster*; actinal plates in longitudinal series parallel to the ambulacra, the largest plates and longest series adradial, naked or armed with a few spaced spines; adambulacral plates with two series of spines sheathed in thick skin: pedicellariae present in some species, granuliform or (in *Petricia* and *Valvaster*) large bivalved

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(*Valvaster* also having some elongated tong shaped ones): internally interbrachial septa present and reinforced by a proximal vertical calcified column in each interradius, joined to the side wall of the disc by a membrane (in *Asteropsis* at least; septum present but undescribed by Fisher, 1911 in *Dermasterias* and in *Valvaster* by Blake, 1980).

Discussion: In distinguishing between the Asteropseidae and Poraniidae in 1976, Hotchkiss & Clark (p. 266) failed to realize that *Poraniella* Verrill, 1914 (then unrepresented in the British Museum collections) shares the arrangement of the series of actinal plates parallel to the furrow characteristic of the Asteropseidae, to which this west indian genus is now referred from the Poraniidae as the only Atlantic representative of an otherwise Indo-Pacific family. All the known specimens of *Poraniella* are small, whereas the other asteropseids may exceed 70 mm or even 100 mm R.

In comparison of a *Poraniella echinulata* (Perrier) (from the *Pillsbury* collections in the Lesser Antilles) with a small *Asteropsis carinifera* (Lamarck) (from the Indian Ocean), both R *c.* 10 mm, the abactinal plates are similarly arranged in longitudinal rows and hexagonal in shape, though with slightly better developed and more imbricating lobes in *Poraniella* where there is a well developed armament of fine spaced spinelets or spines on the abactinal, marginal and actinal plates missing in the *Asteropsis*. Both have the five primary radial plates distinctly enlarged at the head of the midradial series of plates which form a keel in the *Poraniella* whereas, surprisingly, the rays are quite flat in the small *Asteropsis* though keeled in larger ones. Also the superomarginals of the small *Asteropsis* completely overlie the inferomarginals, rather than being inset as in *Poraniella,* and each bears a relatively stout tubercular spine and some smaller tubercles, though in large *Asteropsis* these plates are inset and usually naked. The skin investment is thicker throughout in the *Asteropsis* but the wet preservation (the *Poraniella* is dry) may account for the difference.

Because of the general resemblance of the plating at some stage of the ontogeny, I do not think that the difference in armament and apparently thinner skin in the *Poraniella* merit more than a generic difference, justifying its inclusion in the Asteropseidae. Indeed, *Poraniella* is intermediate in armament and skin between *Asteropsis* and *Valvaster,* supporting Blake's inclusion of *Valvaster* in the family in 1980.

Family **PORANIIDAE** Perrier

Poraniidae Perrier, 1893: 849; 1894: 163–164; Verrill, 1914: 17; 1915: 68; Mortensen, 1927: 89–90; Fisher, 1940: 154; Spencer & Wright, 1966 (pt): U69; Hotchkiss & Clark, 1976: 263–266; Blake, 1981: 380–381.
Gymnasteriidae: Bell, 1893: 21, 78; Farran, 1913: 16.
Asteropidae (pt) Fisher, 1911: 247–248.
Asteropidae: Koehler, 1921: 40–41; Mortensen, 1933: 249: Fisher, 1940: 136.

A family of normally five-rayed Valvatida with body form short-rayed stellate or almost pentagonal, interradial arcs rounded, or sometimes angular (in *Poraniopsis* and some *Poraniomorpha*); upper side arched, under side flat or, if the body is cushion shaped, slightly convex, a ventrolateral angle more or less distinct; dorsal body wall thickened and skin opaque in all but the smallest specimens; abactinal plates obscured or concealed, when well developed either similar and forming an irregular fairly compact reticulum (*Poraniomorpha*) or with the ten primary calycinal plates on the disc enlarged and making a pentaradiate pattern from which run irregular carinal (midradial) series of plates linked to the superomarginals by transverse chains of dorsolateral plates sometimes interconnected to form an open reticulum with larger nodal plates (*Porania* and *Poraniopsis*), but in some taxa the plates progressively resorbed internally, even completely lost in large specimens, R> 50 mm, and the body wall more or less thickened to give compensatory support, gross armament usually lacking or sparse, only *Poraniopsis* and occasional *Porania* with coarse spaced spines on some of the larger plates, sometimes the skin of the upper side with more or less numerous spiniform, papilliform or almost granuliform spinules, forming a continuous coating, rarely even finer

spicules, this superficial armament not necessarily penetrating the soft tissue to contact the underlying plates; papulae either spaced or clustered, often present intermarginally as well as abactinally; marginal plates either well developed together with the abactinal skeleton (though often becoming hollow) or sharing in general decalcification, when well developed the two series tending to alternate and often flattened in planes at right angles, the inferomarginals then horizontal and alone supporting the venterolateral angle, the superomarginals vertical (e.g. in *Porania*) or both series more compact, blocklike, sharing in forming the ambitus, the angle less well marked (*Poraniomorpha*), or the plates relatively undistinguished except for their longitudinal arrangement, the inferomarginals ventrally aligned and without a distinct angle (*Poraniopsis*), inferomarginals armed with a horizontal series, sometimes enclosed within the body wall or more or less aborted (*Porania* and *Chondraster*), or with multiple spinules usually enlarged into spinelets along the maximum convexity (*Poraniomorpha*), or with a few coarse spines not forming a horizontal series (*Poraniopsis*); actinal areas large, the plating obscured by thick skin usually with spaced grooves which sometimes fork or anastomose running from furrow to margin, or pustular, the underlying plates primarily arranged in arcs parallel to the margin, the longest series admarginal (abradial), the shortest adoral, spanning the interradius, also forming series corresponding to the grooves, if the skeleton is generally reduced then the actinals are progressively resorbed from within, appearing as rings on the inner face of the body wall of dissected specimens, the last traces of them close to the adambulacrals, actinal surface either naked or armed with a few spaced spines arising from the underlying plates tending to form series parallel to the margin, or with spinelets enlarged from spinules, spinules alone or unarmed; adambulacrals armed with a few sheathed furrow and subambulacral spines, aligned either transversely (e.g. *Porania*) or longitudinally (*Chondraster* and *Poraniomorpha*); pedicellariae unknown; internally interbrachial septa developed, reinforced by vertical plating unless the entire skeleton is reduced.

Discussion: Hotchkiss (in Hotchkiss & Clark, 1976: 265–266) was largely responsible for emphasizing the importance of the different arrangement of the actinal plates with the primary series either parallel to the margin as in the Poraniidae, or parallel to the furrow as in the Asteropseidae. The two families are also probably distinguishable by thermal differences since the Asteropseidae are found in shallow water in tropical or warm-temperate seas while the Poraniidae are mainly from cold temperate and boreal seas, only occurring in lower latitudes at greater depths and with a stunted form. This accords with the removal now from the Poraniidae to the Asteropseidae of the west indian *Poraniella* Verrill, 1914, because of the actinal plating, which is known from a minimum depth of only 20 m compared with *c.* 175 m for *Marginaster pectinatus* Perrier, the only poraniid from the same area.

Observation of this same character, agreeing conversely with the Poraniidae, in the genus **Poraniopsis** by Blake (pers. comm.) prompted him to suggest that it be removed from the Echinasteridae to this family. Perrier (1891: K106–107) failed to describe the arrangement of the actinal plates but Madsen (1956: 29) noted that their spines run parallel to the margin. Perrier thought *Poraniopsis* intermediate between *Echinaster* and *Porania,* emphasizing this by using *echinaster* as a specific name for the type species. Although he cited more characters in which *Poraniopsis* resembles *Porania,* more weight must have been given to those such as arm shape shared by *Echinaster.* Fisher (1911: 261) thought that resemblances to *Porania* are 'mostly superficial', holding to this view still in 1940 (pp. 154–155) when faced with an unusually well-armed Falkland Is specimen of *Porania antarctica* (Fig. 1B). However, I find there are also important internal characters in which *Poraniopsis* agrees better with *Porania* than with *Echinaster*, comparing specimens from the vicinity of southern South America, as summarized in Table 1. The abactinal plating is very similar, with the primary calycinal plates forming a pentaradiate pattern on the disc in both and irregular midradial (carinal) series forming part of an open reticulum; some nodal plates bear large spines and there are often superficial spinules in the skin. The latter are better developed in the truly antarctic subspecies *P. antarctica glabra* though minute ones *c.* 0·25 mm long are present

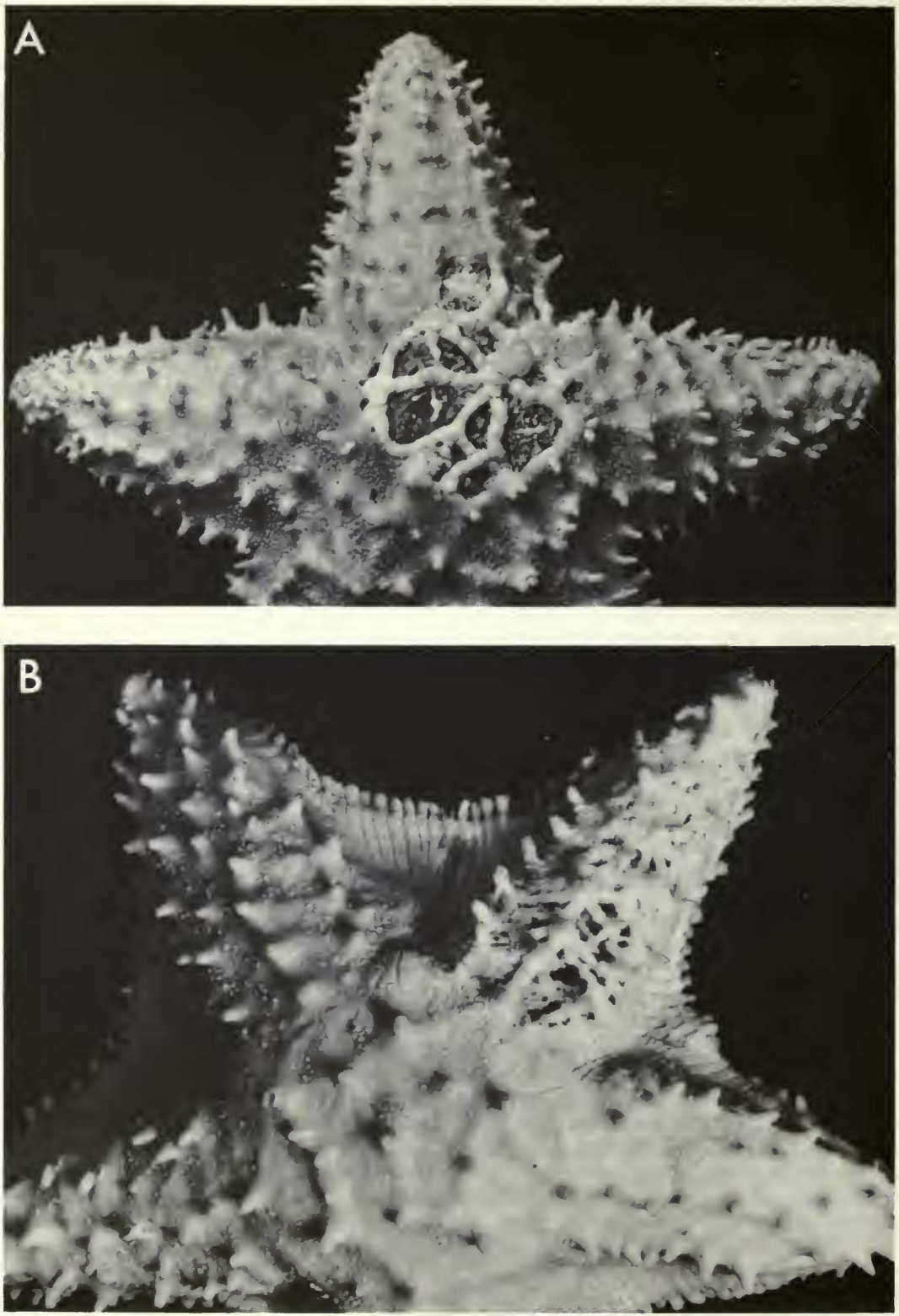


Fig. 1 A. *Poraniopsis echinaster* Perrier, BM reg. no. 1975.11.12.9, Chinquihue, S Chile, R 36 mm; dry, partly denuded, showing spinules between the spines. ×2. B, *Porania* (*Porania*) *antarctica magellanica* Studer, 1948.3.16.448. *Discovery* Investigations st. 80, Falkland Is, R 60 mm; wet, showing papulae between the spines, the spinules microscopic. ×1½.

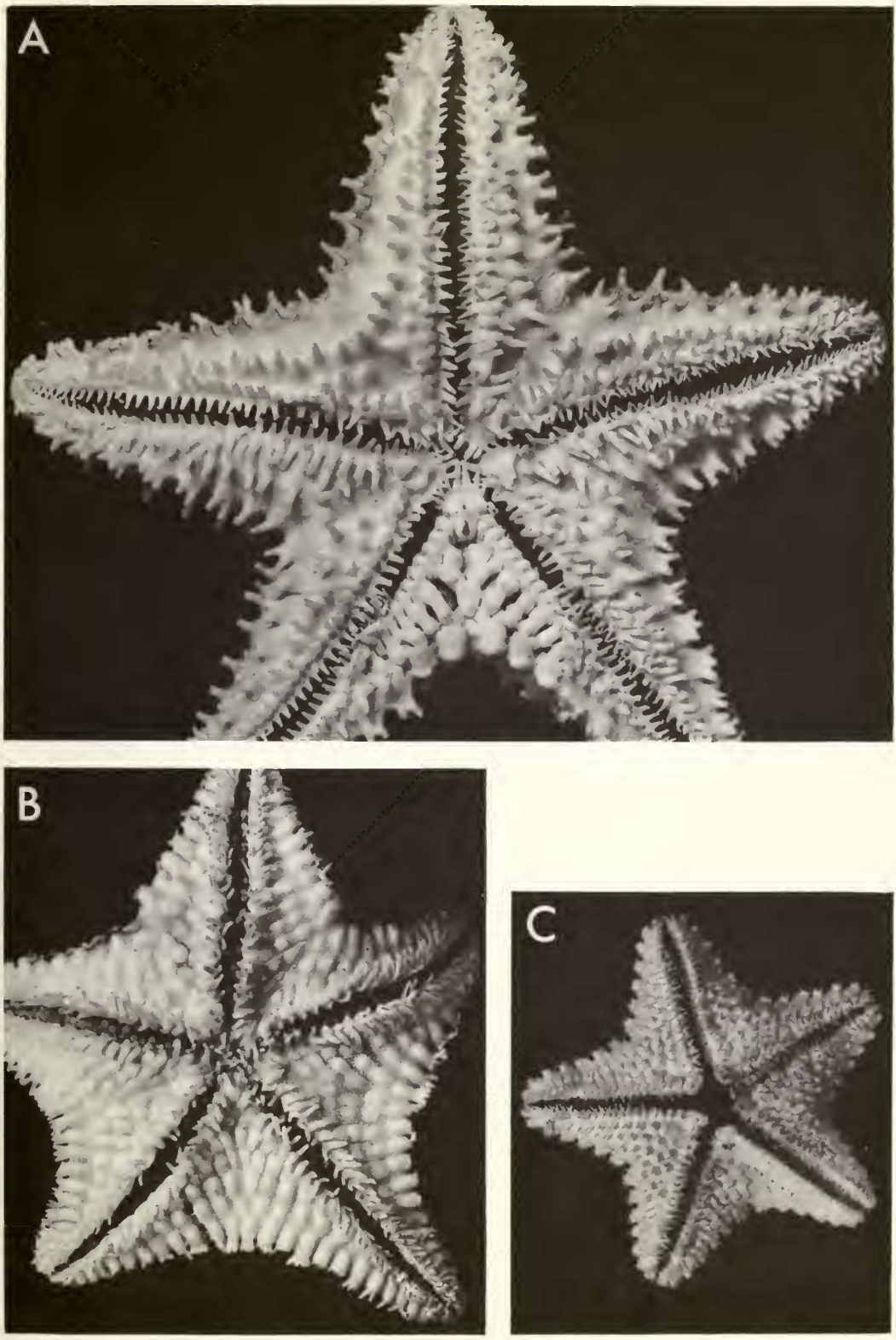


Fig. 2 A, *Poraniopsis echinaster* (as in 1A), partly denuded. ×2. B, *Porania* (*Porania*) *pulvillus* (O. F. Müller), 1922.4.10.1, Lousy Bank, SW of Faeroe Is, R *c.* 36 mm; wet but contracted, the contours of the plates showing their limits. ×1½. C, *Poraniella echinulata* (Perrier), *Pillsbury* st. 853, Windward Is, R 10 mm; dry, partly denuded. ×3.

Table 1 Comparison of *Poraniopsis* with *Porania* (especially *P. antartica*) and *Echinaster*. Agreement with *Porania* in capitals.

	Porania	*Poraniopsis*	*Echinaster*
1	r	a	a
2	C	C	I
3	S	S	N
4	d	u	u
5	a	r	r
6	M	M	L
7	D	D	S

1. Interradial arcs:
   a angular
   r rounded
2. Primary calycinal plates:
   C conspicuous when denuded, linked to form a pentaradiate pattern
   I inconspicuous
3. Skin:
   S usually containing a fine superficial secondary armament of small scattered spinules independent of the underlying plates
   N nude, armament limited to spines mounted on the plates
4. Superomarginal plates:
   u relatively unspecialized, similar to the abactinal plates though corresponding in number to the inferomarginals; usually armed with one or more spines
   d distinct from the abactinals; spineless
5. Profile of ambitus (widest part of body):
   r rounded, curving into the upper and lower sides; inferomarginals inset somewhat on the ventral side, their spines not forming a continuous fringe
   a angular, the prominent ventrolateral angle emphasized by a prominent fringe of spines
6. Alignment of actinal plate series and any coarse armament:
   M in arcs across the interradii parallel to the margin, the admarginal series the longest
   L in longitudinal lines along each ray parallel to the furrow, the adradial series the longest
7. Adambulacral plate joint faces:
   D with a deep restricted interadambulacral muscle depression towards the furrow face
   S with a shallow extensive muscle depression.

Characters 6 and 7 carry the greatest weight in my opinion.

in the Falklands specimen. There is also frequent alternation of the plates of the two marginal series of both *Poraniopsis* and *Porania* and the adambulacral spines are very few, thickly sheathed in skin and aligned at right angles to the furrow, besides the most obvious resemblances of the thick opaque skin and the actinal plate arrangement. Sectioning of an arm shows that the proximal face of the adambulacral plates in *Poraniopsis* has a similarly deep interadambulacral muscle depression towards the furrow side to that found in the poraniids examined, quite different from the much wider and more shallow depression in *Echinaster* (see Blake, 1981, fig. 2, *Chondraster* and *Echinaster*, also Figs 7, 8 here). The main differences in *Poraniopsis* consist of the better-defined rays with an angular rather than curved-interradial arc, the resemblance in shape and armament of the superomarginal plates to the primary (nodal) abactinals and the absence of a distinct ventrolateral angle, the inferomarginals having no horizontal abradial prolongation being instead slightly inset ventrally with the spines of consecutive plates quite discrete, not forming a continuous horizontal fringe. Although the diagnosis of the Poraniidae needs to be somewhat modified to accommodate it, the balance of evidence, I believe strongly supports the inclusion of *Poraniopsis*. Madsen (pers. comm.) tells me that Mortensen placed *Poraniopsis* in the Asteropidae (then including Poraniidae) in the MS catalogue of asteroids in the Zoological Museum, Copenhagen, giving a clue to this disposition by placing *Poraniopsis* after *Chondraster elattosis*, well separated from the Echinasteridae in his table of south african echinoderms (1933: 225). Leipoldt (1895) also concluded that *Poraniopsis* belongs in the Poraniidae but this has generally been overlooked.

Ten other nominal genera of poraniids are known from Atlantic waters. With the currently accepted name of the type species, these are:

Porania Gray, 1840. *P. pulvillus* (O. F. Müller, 1776) (as *Asterias*)
Poraniomorpha Danielssen & Koren, 1881. *P. hispida* (M. Sars, 1872) (as *Asterina*)
Tylaster Danielssen & Koren, 1881. *T. willei* Danielssen & Koren, 1881
Marginaster Perrier, 1881. *M. pectinatus* Perrier, 1881
Chondraster Verrill, 1895. *C. grandis* (Verrill, 1878) (as *Porania*)
Culcitopsis Verrill, 1914. *C. borealis* (Süssbach & Breckner, 1911) (as *Culcita*)
Poranisca Verrill, 1914. *P. lepidus* Verrill, 1914
Pseudoporania Dons, 1936. *P. stormi* Dons, 1936
Sphaeriaster Dons, 1939. *S. berthae* (Dons, 1938) (as *Sphaeraster*)
Spoladaster Fisher, 1940. *S. brachyactis* (H. L. Clark, 1923) (as *Cryaster*).

Two of these, **Marginaster** and **Poranisca,** are only known from small specimens, R < 20 mm. Verrill (1914: 19) suggests that *M. pectinatus* is probably 'simply the young of *Porania* or some similar genus', while his own *Poranisca* was proposed 'as a matter of convenience for another group of small young forms belonging to this family, until they can be connected with adults'. However, Downey (1973: 81) found some of the small Marginasters from the West Indies to be sexually mature. It is not clear from Verrill's account just how he thought *Poranisca lepidus* differs from *Marginaster.* His photograph of the largest (syn) type (1914, pl. 1, fig. 3a) is remarkably similar to the specimen of *M. pectinatus* figured by Downey (1973, pl. 37, fig. A). Both have fairly numerous coarse abactinal spines. Verrill wrote: 'the type is from off the eastern coast of the United States, in 77 fathoms, no, 18,485, Nat. Mus.' A specimen with this catalogue number sent to me as a 'Type' of *Marginaster austerus* Verrill, 1899, was originally so identified by Verrill but subsequently he wrote '*Por. lepidus* V. Type' on the back of the earlier label. This label also bears in pencil an illegible *Albatross* station number beginning with 2 over which has been written 'near sta. 2265' the full station data for which are: 37°07′40′′N, 74°35′40′′W (off Chesapeake Bay) 70 fathoms. Since in 1899 (p. 222) *Marginaster austerus* was cited as from *Blake* and *Albatross* stations in *the West Indies* [my italics], in which area many hauls numbered at around 2350 were made, I think it very likely that the substituted number and hence the more northern type locality given for *P. lepidus* were misleading. It is significant that Verrill included no less than eight figures of *Poranisca lepidus* in his 'Starfishes of the West Indies' (1915) without having any mention of the species in his text, while the 'east of the U.S.' locality should have made it completely inappropriate. His plate, 4, fig. 3 shows this specimen, although it was not among the four illustrated in 1914 (pl. 1, fig. 3a-d) some of which have relatively broader inferomarginal plates, leaving little doubt that *lepidus* is a synonym of *Marginaster pectinatus. Poranisca* therefore becomes a synonym of *Marginaster.*

A second *Albatross* specimen in the U.S.N.M. collection labelled as a 'type' of *Marginaster austerus* (cat. no. 10179 from st. 2333, 'off Havana, Cuba, 169 fathoms') proved to be a *Poraniella echinulata* (Perrier, 1881), the actinal plates being aligned parallel to the furrow and the five primary radial plates being conspicuously enlarged and convex. Little, if anything of Verrill's 1899 description of *austerus* could have been based on this specimen.

The only other extant 'type' of *M. austerus* is in the Peabody Museum, Yale (no. 9858) labelled by Verrill 'sta. unknown. West Indies. coll. A.E.V. Two enlarged photos; also drawings'. This has R/r 16–17/10 mm (17/11 according to Verrill, 1915: 78) and is almost certainly the specimen with an abbreviated arm shown in his pl. 3, fig. 1, 1a, captioned as 'type'. Most of his 1899 description (p. 221) could have been based on it except for descriptions of the primary calycinal plates as *distinctly* enlarged and the proximal actinal plates as bearing rows of spinules—both contradicted in his 1914 and 1915 remarks, the latter specifically referring to the type. Accordingly, this specimen is the most appropriate one for selection as lectotype. Superficially it looks rather different from *Marginaster pectinatus* (compare Figs

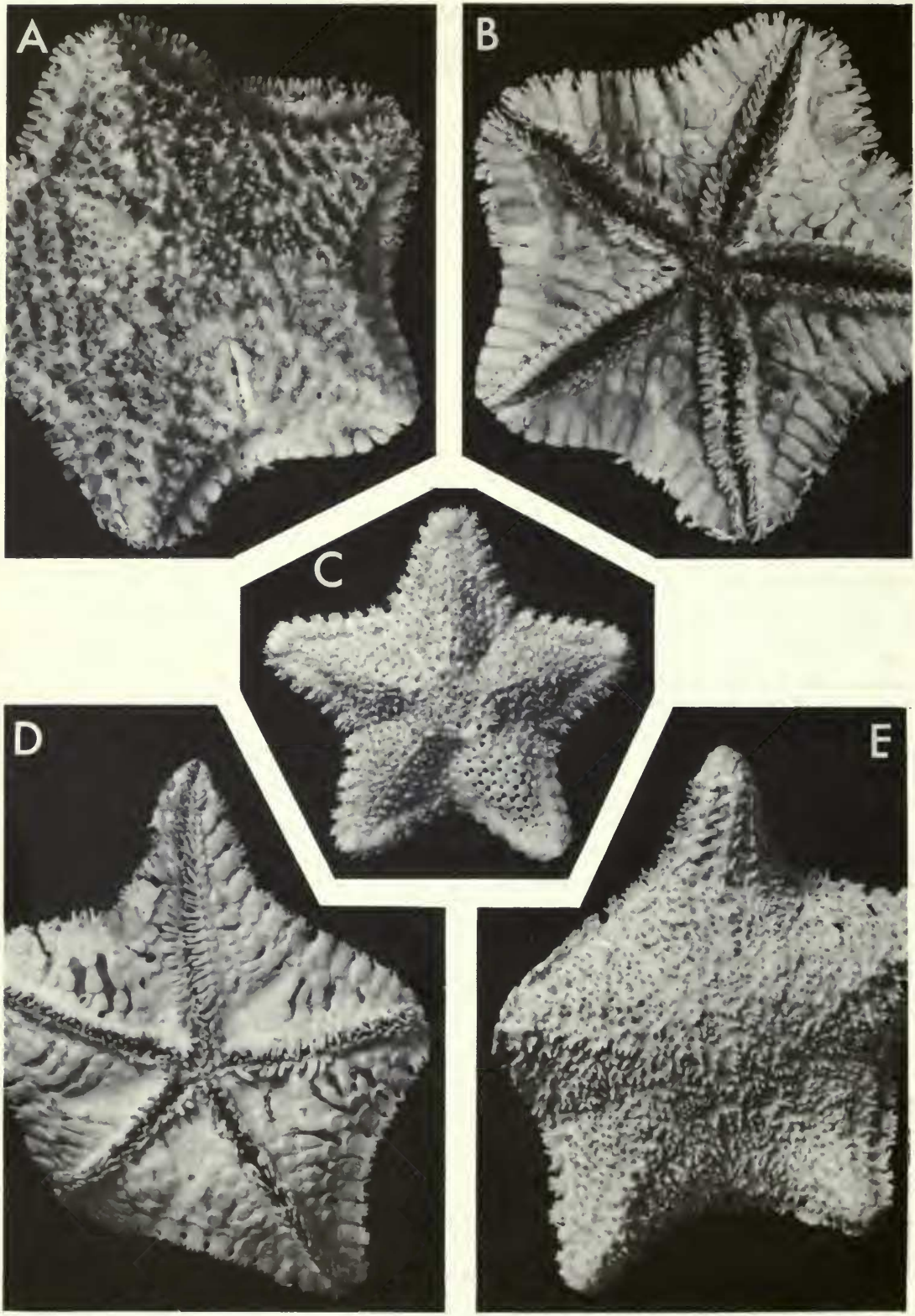


Fig. 3 A, B, *Marginaster pectinatus* Perrier, *Pillsbury* st. 876, Windward Is, R 15 mm; dry, partly denuded. C, *Poraniella echinulata* (as in 2C), dorsal view. D, E, *Marginaster austerus* Verrill, P. M. Yale no. 9858, lectotype, 'West Indies', R 16–17 mm; dry. All $\times 3$.

2C, 3C and 3A, B) notably in the more evenly convex upper side after drying—all the dried *pectinatus* seen being almost flat level with the tops of the superomarginal plates; also the number of marginals is greater, 8–10 rather than 7 or 8 in *pectinatus* of similar size and the inferomarginals project less, forming only an inconspicuous border in ventral view; lastly, the superomarginals in *austerus* are armed with spaced spines for their full height, not just at the upper end, whereas *pectinatus* usually has a bare belt above the inferomarginals, only occasionally a few longer superomarginal spines. The first of these differences may be attributable to an artefact of preservation but the others together could provide a significant difference. However, in general the remaining armament is similar and I suspect that *austerus* will prove to be a synonym of *pectinatus* when more material is available. It should be noted that Verrill's pl. 11, fig. 6a (1915) misrepresents the adradial actinal plates as being in line with the furrow; they are parallel to the margin as usual in poraniids.

There is a further possibility that *Marginaster* itself could be a synonym of *Porania,* to which genus Verrill provisionally referred *austerus* in 1914 (p. 20). In 1895 (pp. 138–139) he wrote of *P. insignis* from east of the U.S.A. 'Young specimens––have more or less numerous small, scattered simple spines, both on the dorsal and ventral plates; these plates are distinctly visible, beneath the cuticle, when dried, and the upper marginal plates are relatively larger than in the adult. The papulae are few and scattered. In this stage, it agrees in all respects with the genus *Marginaster* Perrier and *Lasiaster* Sladen, both of which are probably the young of *Porania* or *Poraniomorpha*'. Possibly *Lasiaster* was added here as an afterthought, since he used the singular 'genus'; it has since been synonymized with *Poraniomorpha.* A proper comparison of *M. pectinatus* with small Poranias from off the USA may shed more light on the relationship and the status of the name *Marginaster.*

As for the even smaller (R max. *c.* 10 mm) geographically 'fringe' species (latitudinally). *Marginaster capreensis* (Gasco, 1876: 38) from the Mediterranean in 50-*c.* 600 metres this is very similar in abactinal and marginal armament to *M. pectinatus* but has more numerous actinal and adambulacral spines. In comparison, the N. european *Porania pulvillus* loses the few actinal spines found in juveniles more quickly than the american *P. insignis.*

A fourth atlantic *Marginaster* is *M. fimbriatus* Sladen, 1889: 365–366, known only from the holotype, R 6 mm, from the Rockall Trough, W of Scotland, in 2487 metres. The name *fimbriatus* was synonymized with *Marginaster capreensis* by Ludwig (1897: 190), prompting Mortensen's inclusion of the latter in the british fauna (1927: 92). However, recent collecting in the Rockall Trough has produced several specimens from down to 2070–2210 m which are much more likely to be the same species although the smallest, R 22 mm, is much larger than Sladen's type. I believe that these are referable to the genus **Chondraster** and conspecific with *Chondraster grandis* (Verrill, 1878: 371–372), known for off Cape Cod to Cape May, U.S.A. in *c.* 400–1645 m. One of Farran's three specimens (from *Helga* st. SR 483) named by him *Culcita borealis* Süssbach & Breckner (1913: 15–16) also proved to be *grandis* besides several others from various sources extending to the Bay of Biscay at *c.* 44°N, 04·5°W. (Biogas VI st. CP 29). Arm sections and X-rays of some of them show a single horizontal row of slender tapering inferomarginal spines, as in *Porania*, numbering up to 4 on a plate, but these are completely enveloped by the very thick body wall, not individually sheathed; only by excessive shrinkage in preservation does their presence become evident externally. The proximal superomarginals are deeply inset, aligned vertical but somewhat obliquely, tall and flattened, exaggerated in form from those of *Porania*, while the inferomarginals are flattened horizontally and markedly elongated at right angles to the edge of the body, the spines usually present borne along their abradial ends (see Fig. 7D). The actinal plates are very elongated and overlap to form series linking the inferomarginals with the adambulacrals. A section of a large specimen, R *c.* 73 mm, shows only a few small, hollow, isolated abactinal plates. X-ray show the density of the other skeletal plates is also low. The adambulacral plates bear usually 2 individually-sheathed furrow spines and 2, sometimes 3, subambulacral spines within a single elongate sheath aligned almost parallel to the furrow, contrasting with the single transverse row in *Porania.* The smallest specimen, R 22 mm, from the southern Bay of Biscay, is dried, which helps to show a better developed skeleton approximating to that

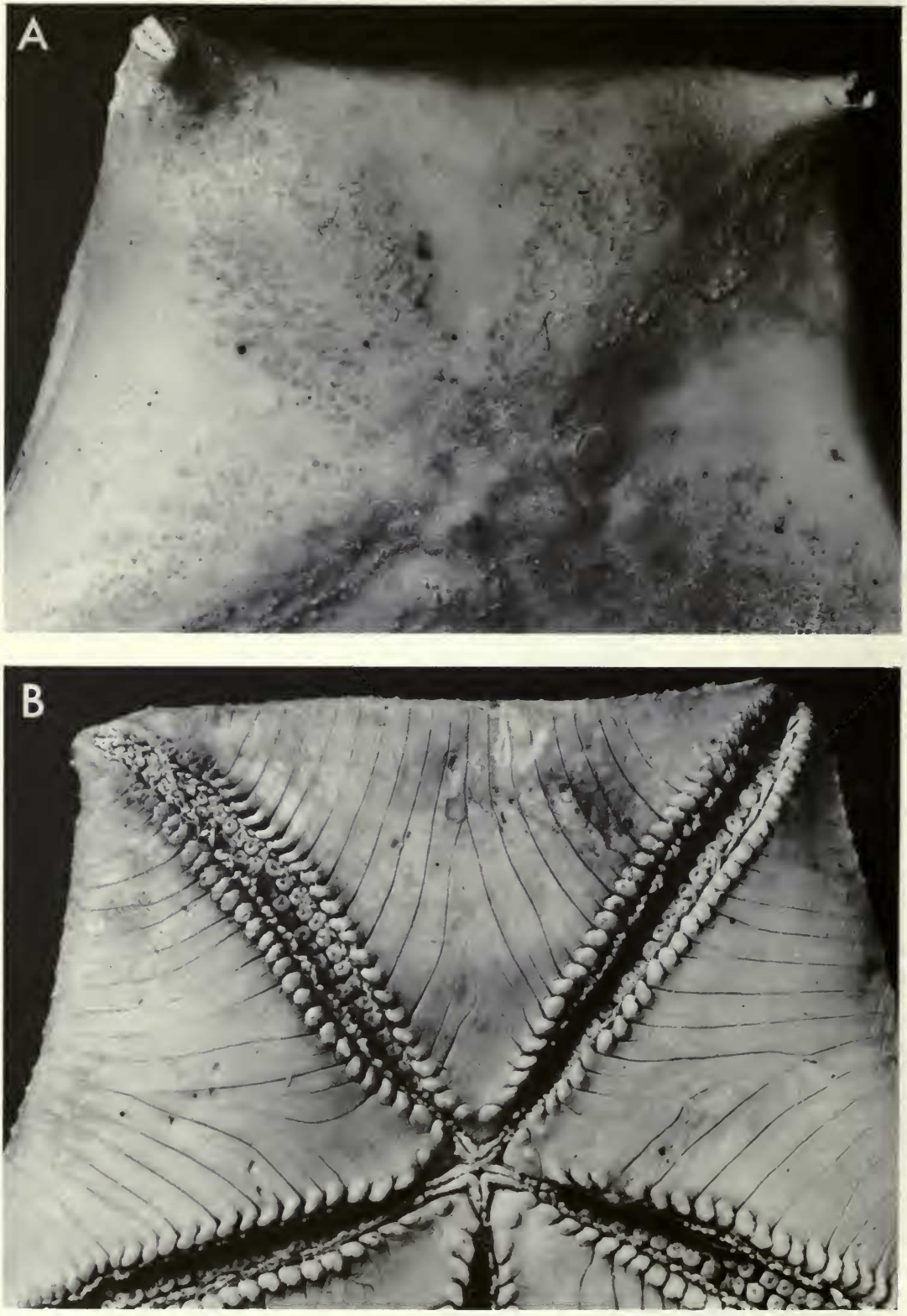


Fig. 4 A, B. *Chondraster grandis* (Verrill), 1981.7.20.1, Rockall Trough, R 73 mm; partial dorsal and ventral views. × 1½.

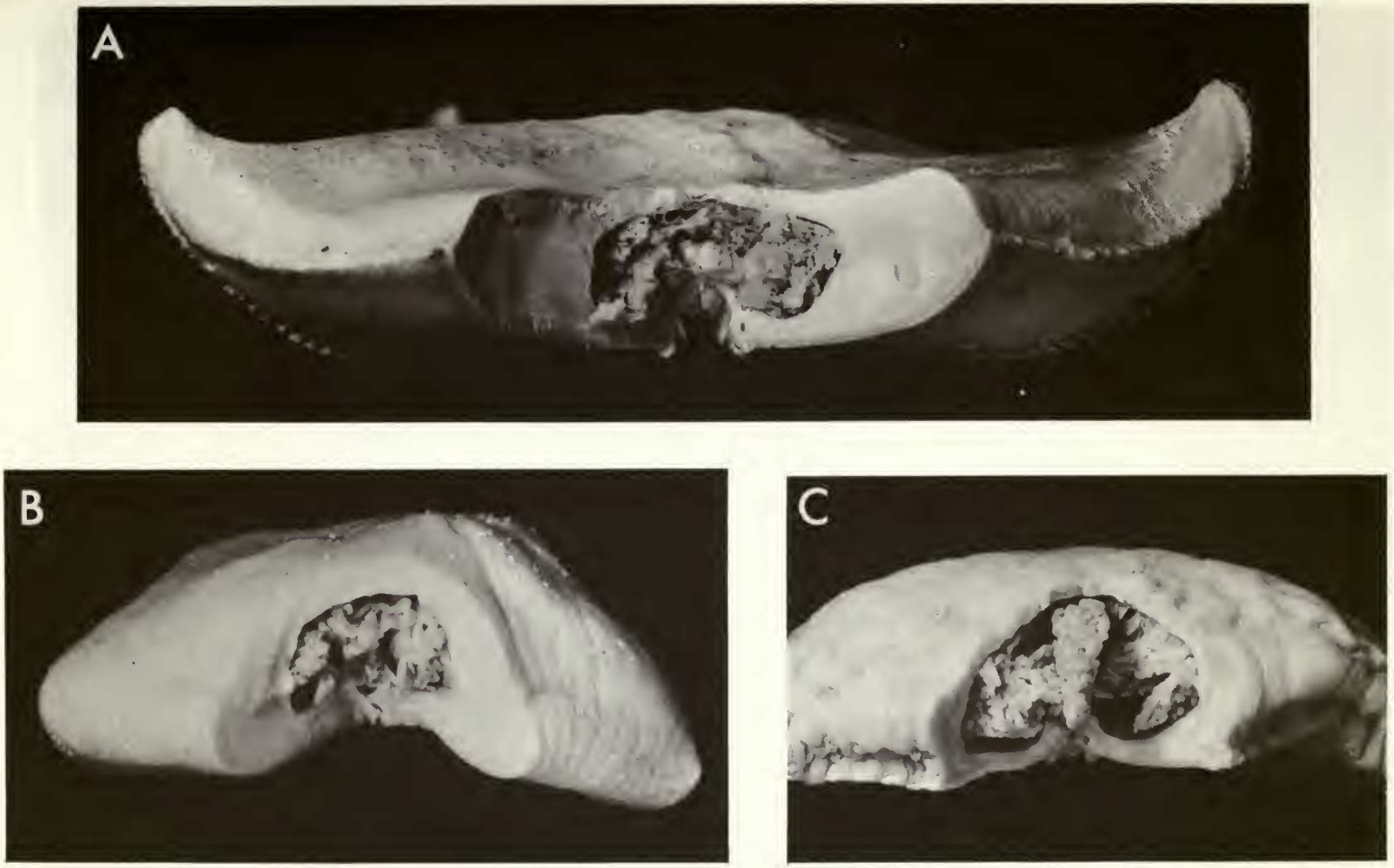


Fig. 5 Side views into the cavity left by severing an arm of: A, *Chondraster grandis* (Verrill) (as in 4A, B). B, *Porania* (*Pseudoporania*) *stormi* (Dons), 1920.12.28.31, Lousy Bank, SW of the Faeroe Is, R 40 mm. C, *P.* (*Porania*) *pulvillus* (O. F. Müller), 1974.11.25.2, Shetland Is, R 52 mm. All wet specimens, $\times 1\frac{1}{2}$

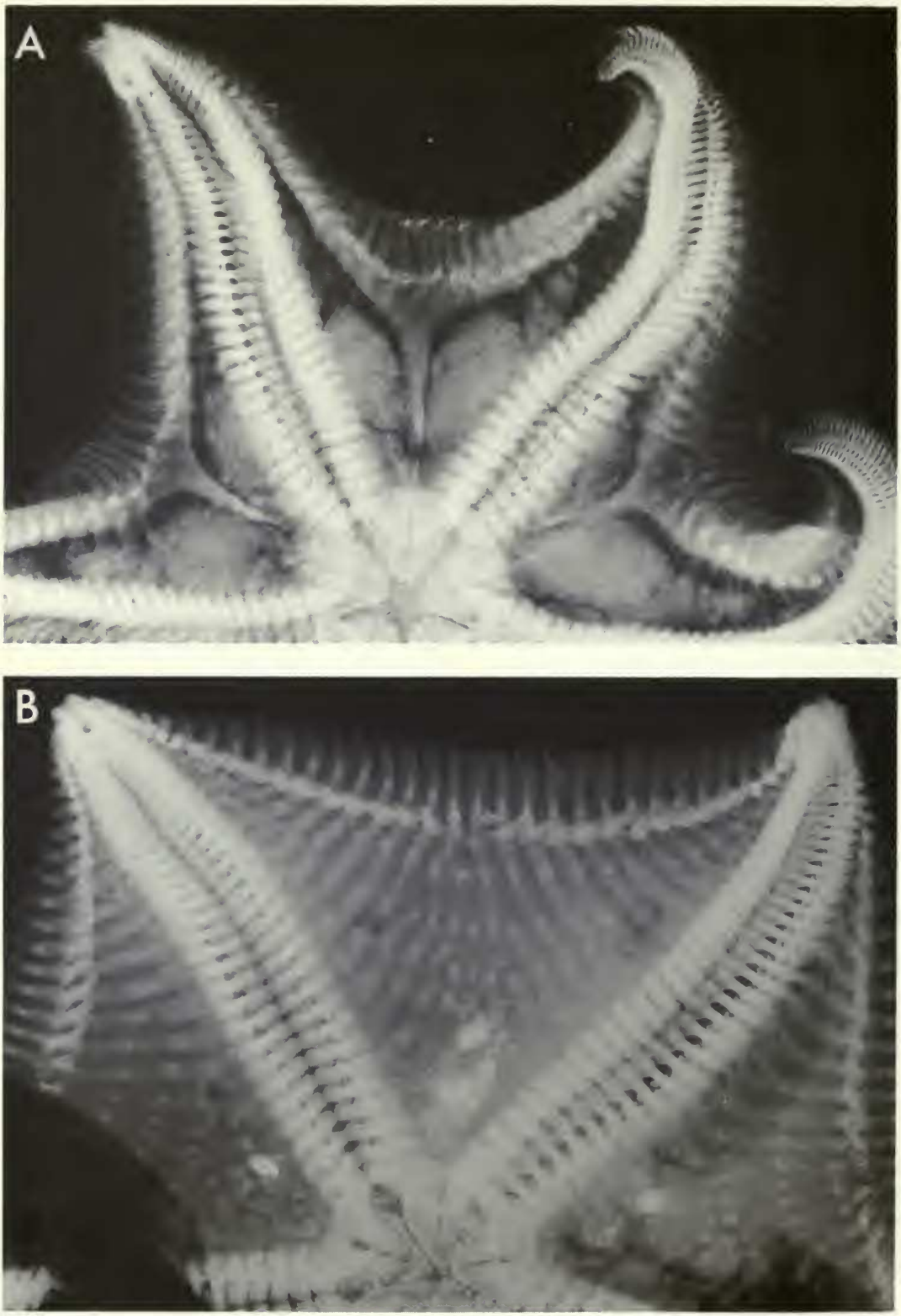


Fig. 6 X-rays of *Chondraster grandis* (Verrill): A, No details, off Cape Cod, specimen probably dried and shrunken, R *c.* 75 mm. B, (as in 4). × 1½.

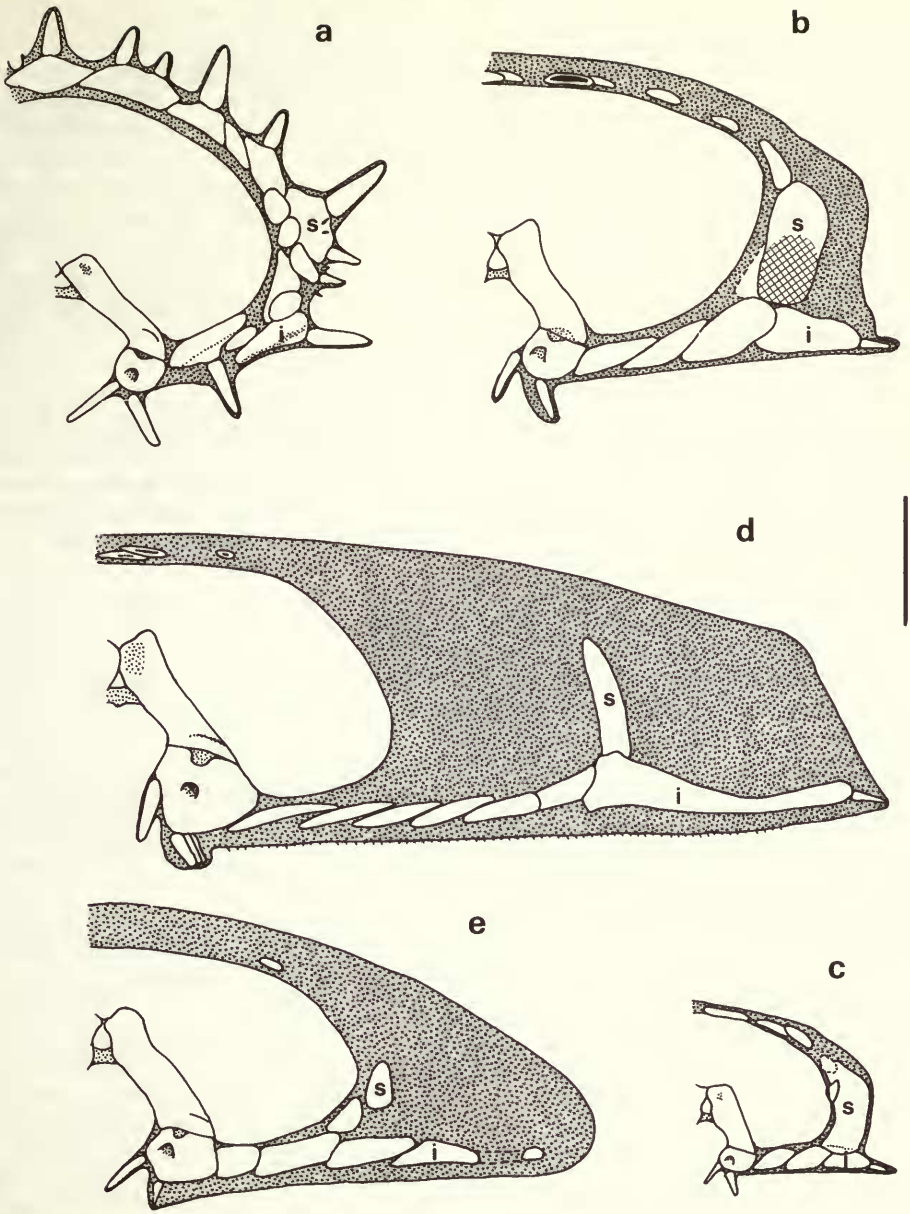


Fig. 7 Partial cross section near base of ray viewed from proximal side of: a, *Poraniopsis echinaster* Perrier, 79.8.19.6, Magellan Strait, R *c.* 37 mm; b, *Porania* (*Porania*) *pulvillus* (O. F. Müller), 1950.11.3.1, Porcupine Bank, W of Ireland, R 55 mm, the cross-hatched area of the second superomarginal hypothetical, the plate cut in sectioning; c, *P. pulvillus,* 90.5.7.511, *Porcupine* st. 8, W of Ireland, R 14 mm; d, *Chondraster grandis* (Verrill), 1981.7.20.1, *Cirolana* st. 22, E side of Rockall Trough, R *c.* 73 mm; e, *Porania* (*Pseudoporania*) *stormi* (Dons), 1920.12.28.31, Lousy Bank, SW of Faeroe Is, R 40 mm, the median part of an adjacent complete inferomarginal plate shown by discontinuous lines. i = inferomarginal, s = superomarginal. The scale measures 5 mm.

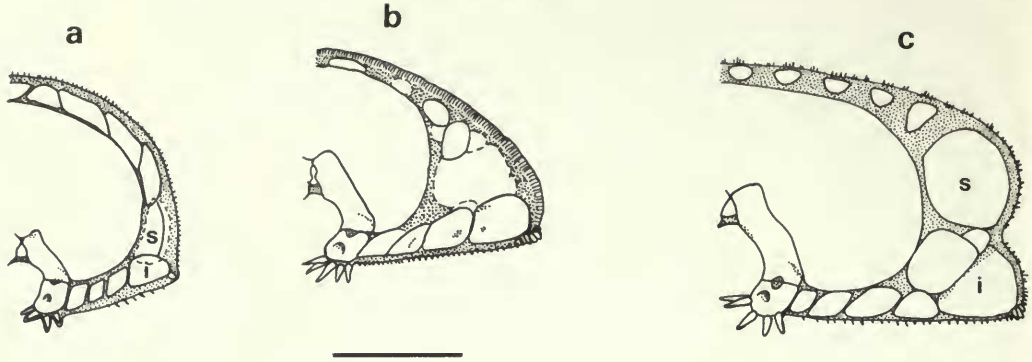


Fig. 8 Partial cross sections near base of ray viewed from proximal side of: a, *Poraniomorpha* (*Culcitopsis*) *borealis* (Süssbach & Breckner), IOS st. 50702, Porcupine Seabight, R 19 mm; b, *P.* (*Poraniomorpha*) *hispida* (M. Sars), 98.5.3.223, Trondheim fjord, R 26·5 mm (inferomarginal armament dubbed from another specimen); c, *P. hispida rosea* Danielssen & Koren, SMBA st. AT 230, Rockall Trough, R 33 mm. Plates well out of the plane of the section are shown by discontinuous lines; i = inferomarginal, s = superomarginal. The scale measures 5 mm.

of *Porania pulvillus* with the primary radial and interradial abactinal plates distinct on the disc and irregular carinal series linked to some of the superomarginals by transverse chains of dorsolateral plates; however, the proximal marginals are of more exaggerated form than in *Porania*. There are 2–4 inferomarginal spines on each plate and 1, sometimes 2, spines on many plates of the adjacent actinal series, as in some adults of the american *Porania insignis* and the arctic *Tylaster willei*. The larger Chondrasters all lack actinal spines and show varying degrees of skeletal reduction. The extent of the papulae is also very variable, from the two narrow bands along each ray shown in Verrill's figure (1885, fig. 44a), to a wide coverage of the upper side except for small midradial and interradial bands; some papulae may even occur between successive superomarginals.

Although these specimens are clearly conspecific with *Chondraster grandis* from the NW Atlantic, they might be subspecifically distinct. An X-ray of an american specimen, R *c.* 75 mm (Fig. 6A), shows discontinuous series of inferomarginal spines, with 1 or 2 on most interradial and some distal plates, not in between. The inferomarginals appear hollow almost to the abradial extremity in contrast to those of the NE Atlantic specimens but vestiges of actinal and possibly some abactinal plates are similarly distinguishable. Another specimen, from Lydonia Canyon, SE of Cape Cod, R *c.* 55 mm, shows up to 3 spines on most inferomarginals but no trace of any abactinal or actinal plates; the marginals themselves are ill-defined, whereas a larger similarly dried NE Atlantic individual (from Lousy Bank, SW of the Faeroes), as well as the large wet Rockall Trough specimen, show quite distinct outlines of many actinal plates at least, indicating that the dried and contracted condition is not responsible for the skeletal loss in the american specimen.

One of Verrill's two syntypes of *C. grandis* has been examined, the second is not to be found in the Peabody Museum, Yale. It is considerably shrunken and flattened with all the rays curled upwards and the distal part of one broken off. Although now in alcohol it may have dried up at some time judging from the extreme flattening and shrinkage of the body wall. Mean R is estimated at *c.* 95 mm; in life it was probably 100+ mm; r is *c.* 50 mm. Superficial spicules all over the upper side give a 'furlike' appearance; on the lower side they are more spaced out, especially proximally. The broken edge of the detached ray shows no sign of any abactinal plates, even in this distal area where resorption is likely to be minimized. However, the actinal plates are still fairly well developed, though hollow, and there are 1–3 spines on the abradial ends of four inferomarginal plates from which the tissue has been pared. Indeed, contours corresponding to actinal plates are evident all over the ventral

interradii, though it does not follow that the plates remain well developed since similar contours may show in poorly preserved specimens of other skeletally deficient poraniids even though X-rays show only vestiges of actinal plates. The papulae are restricted to two narrow bands along each ray, as in Verrill's fig. 44a, 1885, and the same is true of four other american specimens, three of them from Lydonia Canyon, which is on the south side of George's Bank not far WSW from the type locality. R is *c.* 55–105 mm, probably at least 60–120 mm in life since they are dried and very shrunken so that the cluster of spinelets around the anus stands out. The number of subambulacral spines ranges from 2 or 3 in the smallest to usually 4 in the largest and the number of oral furrow spines is 6–8 with a single suboral, except in the smallest specimen which has none.

Verrill initially (1895: 138) treated *Chondraster* as a subgenus of *Porania* but in 1914 (p. 21) evidently accorded it generic rank, being followed in this by H. L. Clark (1923: 274–275) when describing a new species from South Africa. However, in 1959 (p. 160) Madsen thought subgeneric rank to be more appropriate when he described another poraniid, from E Greenland, as *Porania (Chondraster) hermanni.* Since then (pers. comm.) he has come to believe that *hermanni* is a *Porania* sensu stricto and *Chondraster* generically distinct—mainly on account of the longitudinal arrangement of the adambulacral armament in *C. grandis,* whereas *Porania* has these spines in a transverse row.

A final atlantic nominal species of *Marginaster* should be mentioned, namely *M. pentagonus* Perrier, 1882: 51) (also 1894: 165–167, pl. 11, fig. 4), the holotype and only recorded specimen of which had R 3 mm, the body form retaining post-larval flattened shape with the inferomarginal plates (numbering 6 on each side in this specimen) alone forming the periphery, the superomarginals being inset on the upper surface and resembling the somewhat imbricating polygonal abactinal plates, all bearing a scattering of spinelets. The inferomarginals each bear a comb of 6–8 spinelets along the free edge but apparently inclined downwards. On the under side most actinal plates have one or a few small spinelets and the adambulacrals bear a furrow spine and two or three subambulacral spines in a transverse series. Mortensen (1927: 94) and Tortonese (1965: 167) suggest that *pentagonus* could be conspecific with the mediterranean *M. capreensis* but that species has fewer and coarser abactinal spinelets and inferomarginal spines, judging from Ludwig's illustrations (1897, pl. 7, figs 21–23).

The type locality of *M. pentagonus* is NW of Finisterre, Spain (*c.* 44°N, 10·5°W) in 400 metres. The closest geographical record for a poraniid is that of Gallo (1937: 1664) for three specimens from Santander, N Spain, also in 400 m, resembling *Culcitopsis borealis* (Süssbach & Breckner, 1911: 217–218) although he named them *Poraniomorpha hispida* (M. Sars, 1872: 26), following Mortensen's synonymy of *borealis* with *hispida* in 1912 (p. 258) and 1927 (p. 93). The small and relatively numerous inferomarginal spinelets support inclusion of *pentagonus* in **Poraniomorpha** despite the single furrow spines which are probably correlated with the small size. However, the status of **Culcitopsis** needs reassessing since Farran (1913: 15), Koehler (1924: 160–161) and Cherbonnier & Sibuet (1973: 1348) have recorded as *C. borealis* specimens from the Porcupine Seabight (SW of Ireland) and from the NE Bay of Biscay.

Mortensen, and also Grieg (1927: 131) had discounted the swollen form and thickened body wall with reduced skeleton of *C. borealis* as insufficient to warrant more than an infraspecific difference from *Poraniomorpha hispida,* designating such specimens as forma *borealis.* Madsen too (pers. comm.) strongly supports such a low rank, believing that *borealis* is an ecophenotypic form. Certainly most poraniids show some progressive resorption of the skeleton during growth so that even in apparently well-calcified large specimens of *Porania* and *Poraniomorpha* the marginals and other plates may be hollow, as evidenced by sectioning or by X-rays—a useful technique for study of this family of thick-skinned asteroids.

In addition to the above mentioned authors, others have also commented on the considerable variation in several directions of *Poraniomorpha hispida,* notably Djakonov (1946: 163–169, at length, in russian), who compared it with the exclusively arctic *P. tumida*

(Stuxberg, 1878: 31), finding intermediate specimens where the ranges of the two overlap (presumably in N Norway and the Barents Sea), mentioning this briefly in his book on russian asteroids (1950: 59, translation 1968: 50). Unfortunately it is not possible to ascertain the adult form of Sars' material since his holotype (from the Lofoten Is, N Norway, 365–550 m) has R only 6 mm. Although it does have a near pentagonal form, R/r 1·2/1 (see Sars, 1877, pl. 8, figs 24–26), this could be true of a more stellate adult when young. However, Grieg (1927: 129–133) makes several references to the 'typical' form, which by implication is a shorter-rayed one since he also refers separately to forma *rosea,* Danielssen & Koren's holotype of which had R/r 1·67/1 and appears relatively stellate in their figures. Djakonov (1950) also described *P. hispida* as having a massive body, broad disc and broad, very short, rays. In the absence of any evidence to the contrary, this is the form which can be attributed to 'typical' *hispida.* All nine norwegian specimens in the British Museum collections with well developed skeletons (from Hardanger and Trondheim fjords, from SW of Bergen and off the North Cape) consistently have a pentagonal form, R/r 1·3–1·5/1 (R 7–45 mm). Östergren (1904: 615) recognized *rosea* as a distinct variety of *hispida,* followed by Grieg (1907: 42) who noted that specimens from Bergen and Trondheim fjords as well as from Bohuslan in the vicinity of Oslo fjord (i.e. close to shore) are short-rayed whereas those from the deep area of the Skagerrak (500–600 metres) have relatively long rays. The latter form with R/r *c.* 2/1 and triangular rays forming angular interradial arcs was illustrated by Mortensen (1927, fig. 53, taken from his earlier 'Danmarks fauna') but does not appear to be found on the continental shelf in british waters, only from the bathyal at 900–1400 metres to the NW and W of the British Isles, from which *c.* 20 specimens are consistently stellate. These include two small syntypes of *Lasiaster villosus* Sladen, 1889: 372 (synonymized with *Poraniomorpha hispida* by Grieg and others), the specimen from *Helga* st. SR 506 (Fig. 11 B, C) named *P. villosa* by Farran (1913: 17) and others more recently collected in the Rockall Trough and Porcupine Seabight. The only exception is the holotype of *Rhegaster murrayi* Sladen, 1889: 368–371 (Fig. 11 D, E) (another synonym of *P. hispida*) from the Wyville Thomson Ridge in 510–790 metres, which has a near pentagonal form, R/r 1·3/1 but R only *c.* 14 mm. The type locality of *Poraniomorpha rosea* Danielssen & Koren, 1881: 189–192; also 1884: 67–70, the oldest species-group name for stellate european specimens, is NW of Bergen (61°41′N, 03°19′E) in 402 metres, that is in the southern arm of the Norwegian Sea which leads to the Skagerrak. On the basis of this evidence, it is possible that short and long rayed specimens are isolated in different water masses. However, Madsen (pers. comm.) finds considerable overlap in norwegian waters. Nevertheless I believe that *rosea* can be accorded at least subspecific rank.

It should be noted that *rosea* is antedated by two other names long synonymized with *P. hispida,* namely *Asterina borealis* Verrill, 1878: 213–214 and *Porania spinulosa* Verrill, 1880a: 202–203 (Fig. 11F), based on moderately long-armed type material from american waters N and E of Cape Cod. R/r of the respective types is 12/7 = 1·7/1 (implying a higher value when fully-grown) and 40/23 = 1·75/1. Paucity of american material for comparison prevents a proper assessment of the affinites of specimens from east and west and I can only note that the american ones appear to have the interradial arcs more curved and the tips of the rays blunter than is usual in european ones. In 1895 (p. 139) Verrill noted that *spinulosa* was taken 'mostly in the warm area' and *borealis* in the 'cold area' but in 1880 (b: 401) he had recorded both from USFC stations 869 and 879 and in 1914 (p. 18) he remarked that his 1895 notes (p. 139) on a relatively large specimen (R/r 35/23 mm) from the Fishing Banks (*c.* 45·5°N, 57°W, in 170 fathoms) refer not to *borealis* but to *spinulosa.* With such confusion and overlap it is impossible to assess if two infraspecific taxa exist in american waters until more material is available.

With regard to the decalcified adult specimens such as have been referred to *Culcitopsis borealis* (Süssbach & Breckner), the range of these appears to parallel to a great extent that of *P. hispida rosea.* Twelve samples range from the Porcupine Seabight W of southern Ireland N and E to the Faeroe Channel, Shetlands and N Norway (Lofoten Is) in depths down to *c.* 1000 metres though with a minimum of only 110 metres. These show a near-

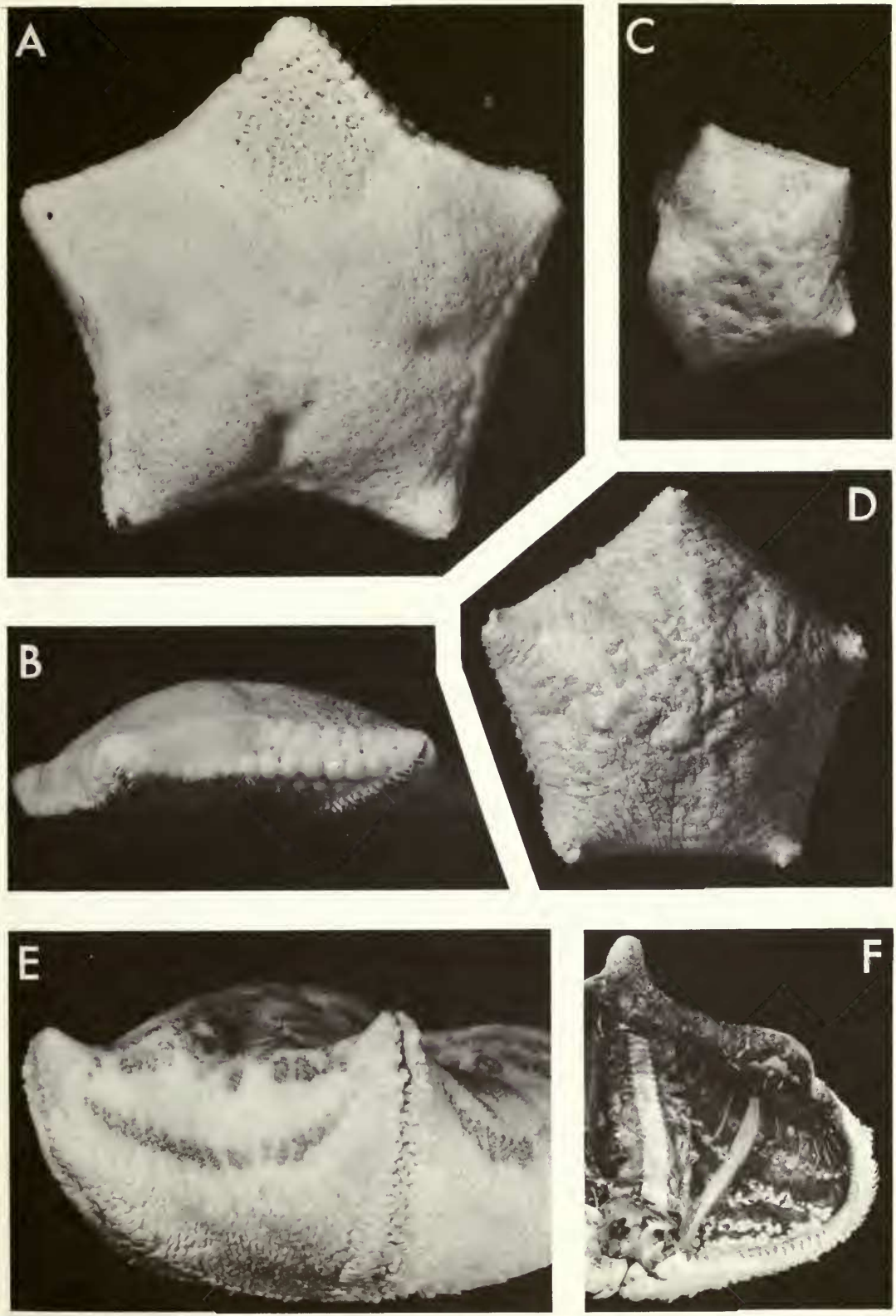


Fig. 9 A, B, *Poraniomorpha* (*Poraniomorpha*) *hispida* (M. Sars), 91.4.15.1, Trondheim fjord, R 32 mm, dorsal and side views, partly denuded. C-F, *P.* (*Culcitopsis*) *borealis* (Süssbach & Breckner): C, (as in 8a); D, 1956.5.25.5, E of Shetlands, R 25 mm, both dorsal views; E, F, 1974.1.4.2, E of Wyville Thompson Ridge, R *c.* 44 mm, side views, E wet, external; F dry, internal. Others all wet, × $1\frac{1}{2}$.

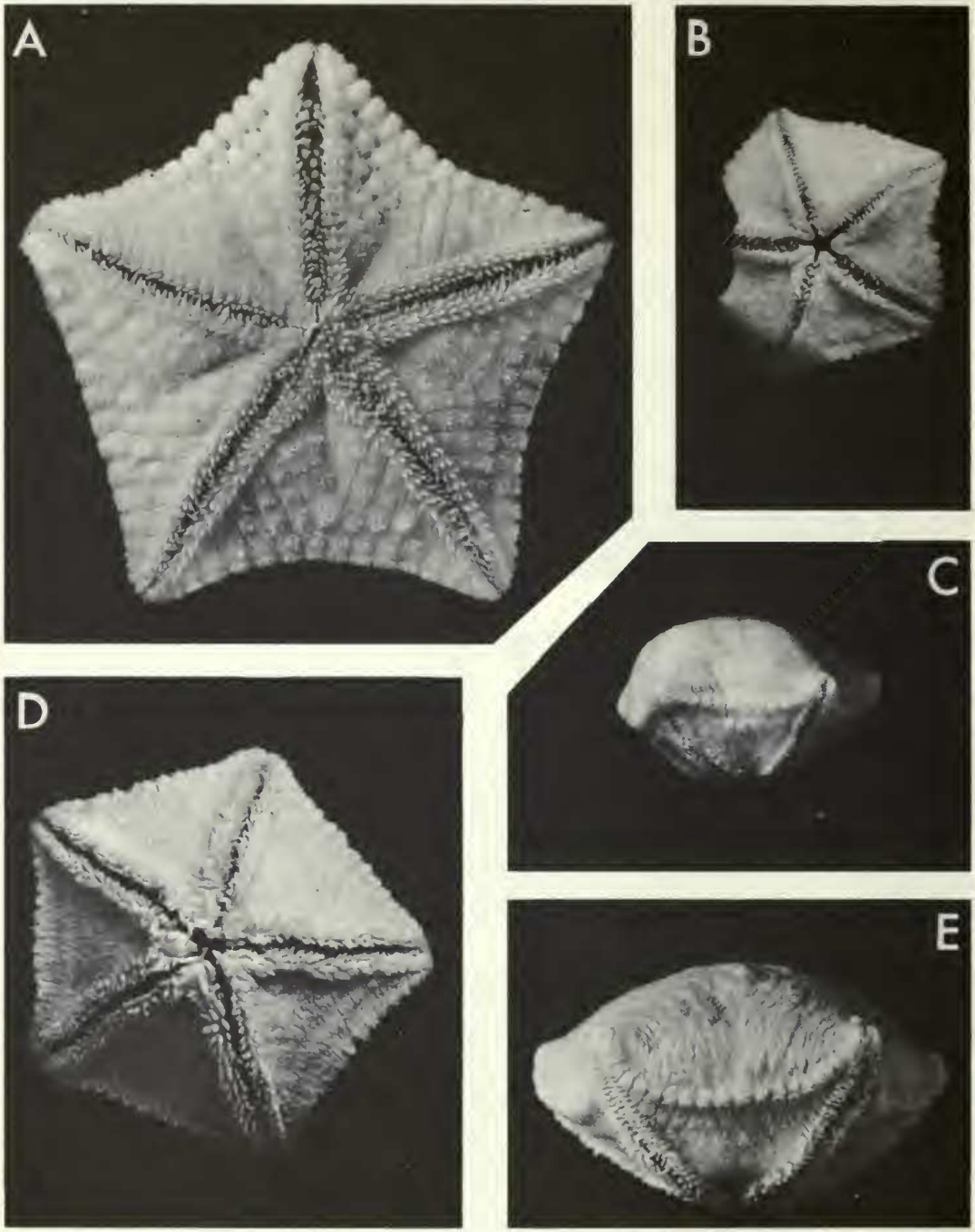
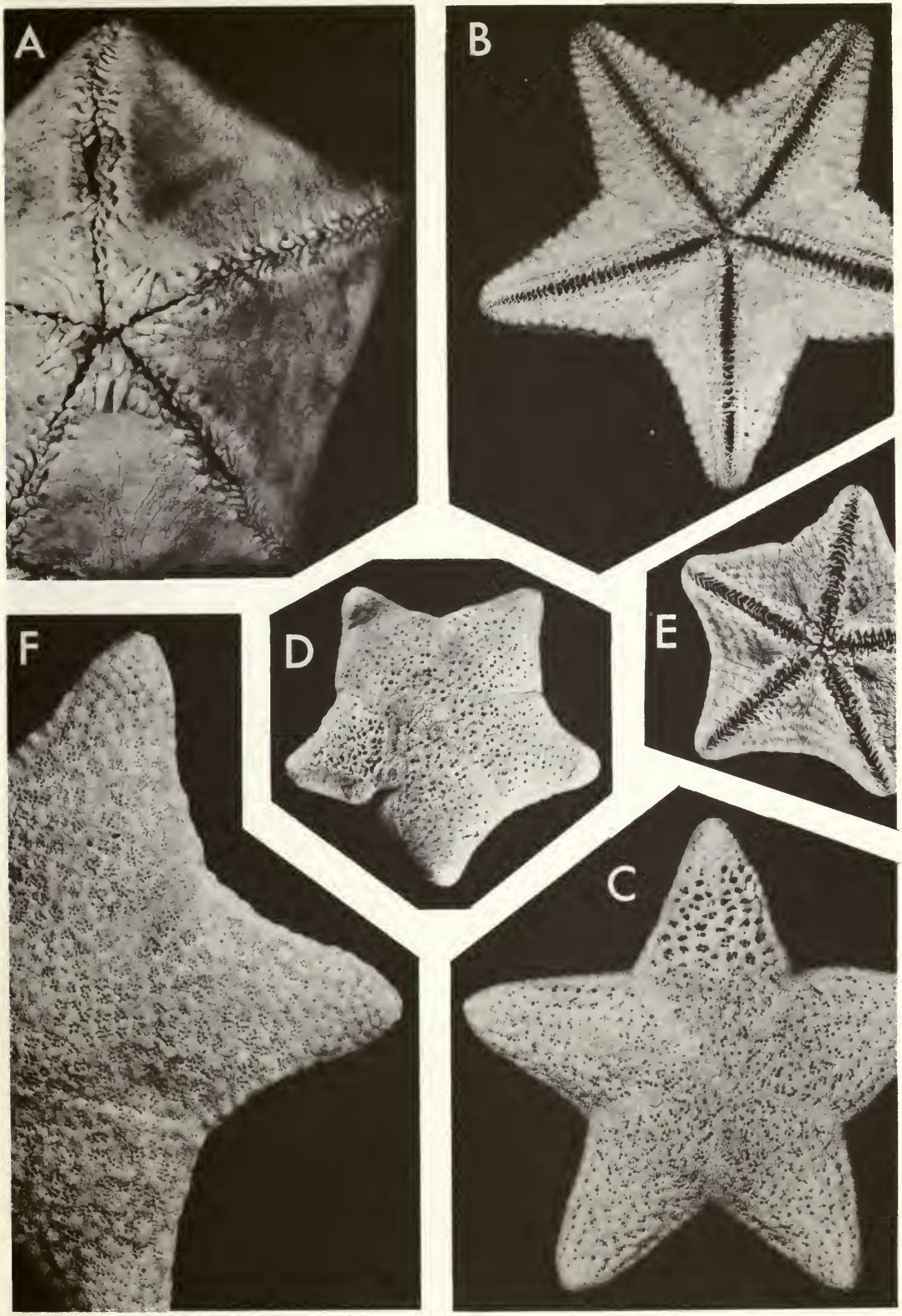


Fig. 10 A, *Poraniomorpha* (*Poraniomorpha*) *hispida* (M. Sars) (as in 9A, B), ventral view. B–F, *P.* (*Culcitopsis*) *borealis* (Süssbach & Breckner): B, C, (as in 8a) ventral and side views; D, E, (as in 9D) ventral and side views. All wet, $\times 1\frac{1}{2}$.

Fig. 11 A, *Poraniomorpha* (*Culcitopsis*) *borealis* (Süssbach & Breckner), National Museum of Ireland no. 102.1913, *Helga* st. SR 223, R *c.* 40 mm, ventral view. B,C, *P.* (*Poraniomorpha*) *hispida rosea* Danielssen & Koren, Nat. Mus. Ireland 403.1913, *Helga* st. SR 506, R 28 mm, ventral and dorsal views. D-F, *P. hispida hispida* (?): D, E, holotype of *Rhegaster murrayi* Sladen, 90.5.7.545, *Triton* st. 5, Wyville Thomson Ridge, R *c.* 14 mm, dorsal and ventral views; F, presumed holotype of *Porania spinulosa* Verrill, Peabody Museum, Yale no. 9867, off Cape Cod Light, R 40 mm. A, wet; others dry; D, E $\times 2$; others $\times 1\frac{1}{2}$.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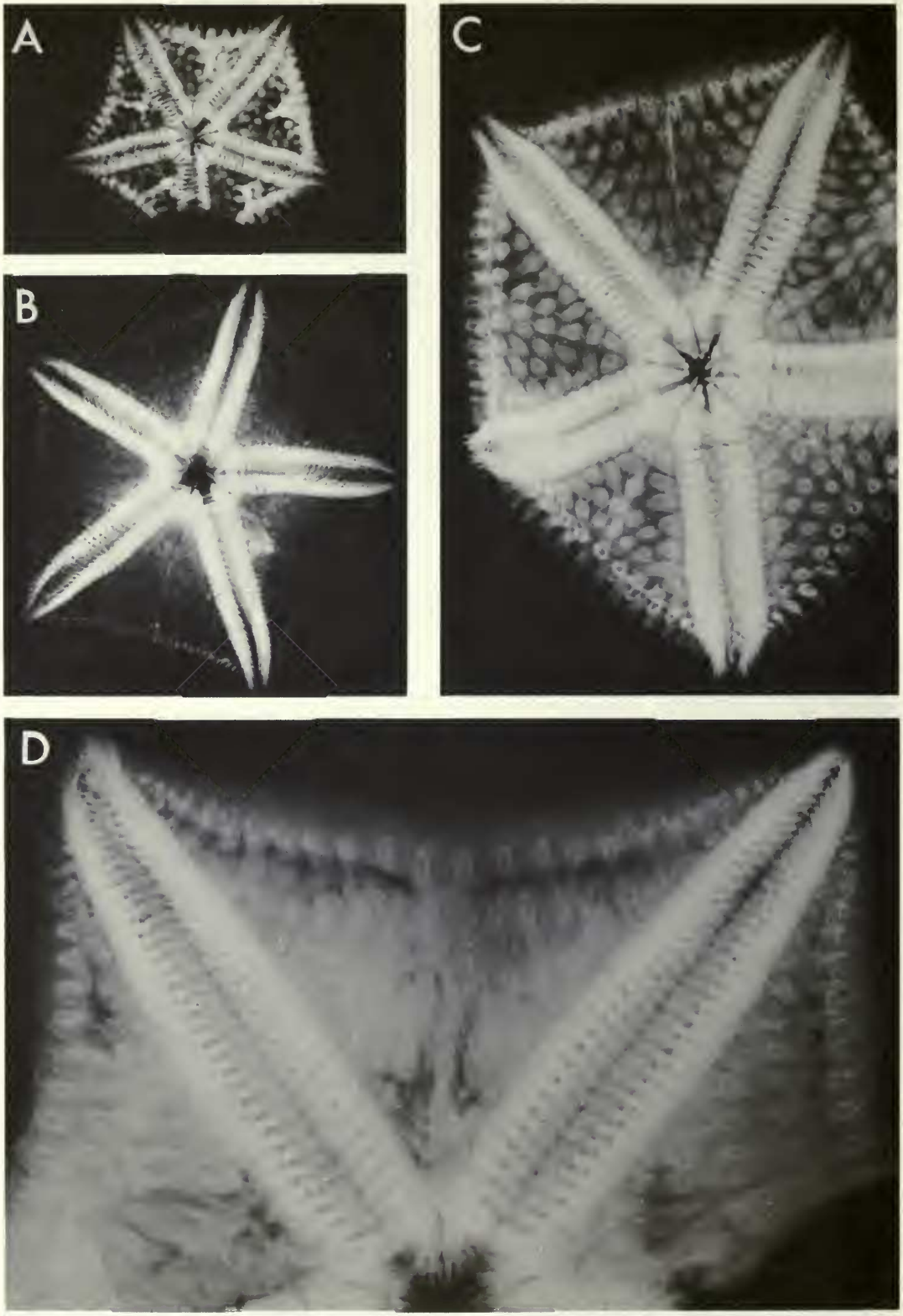

Fig. 12 X-rays of *Poraniomorpha* (*Culcitopsis*) *borealis* (Süssbach & Breckner): A (as in 8a); B (as in 9D); C, IOS st. 50601, Porcupine Seabight, R 35 mm; D, 1965.5.24.4, Lofoten Is, R. *c* 72 mm. × 1½.

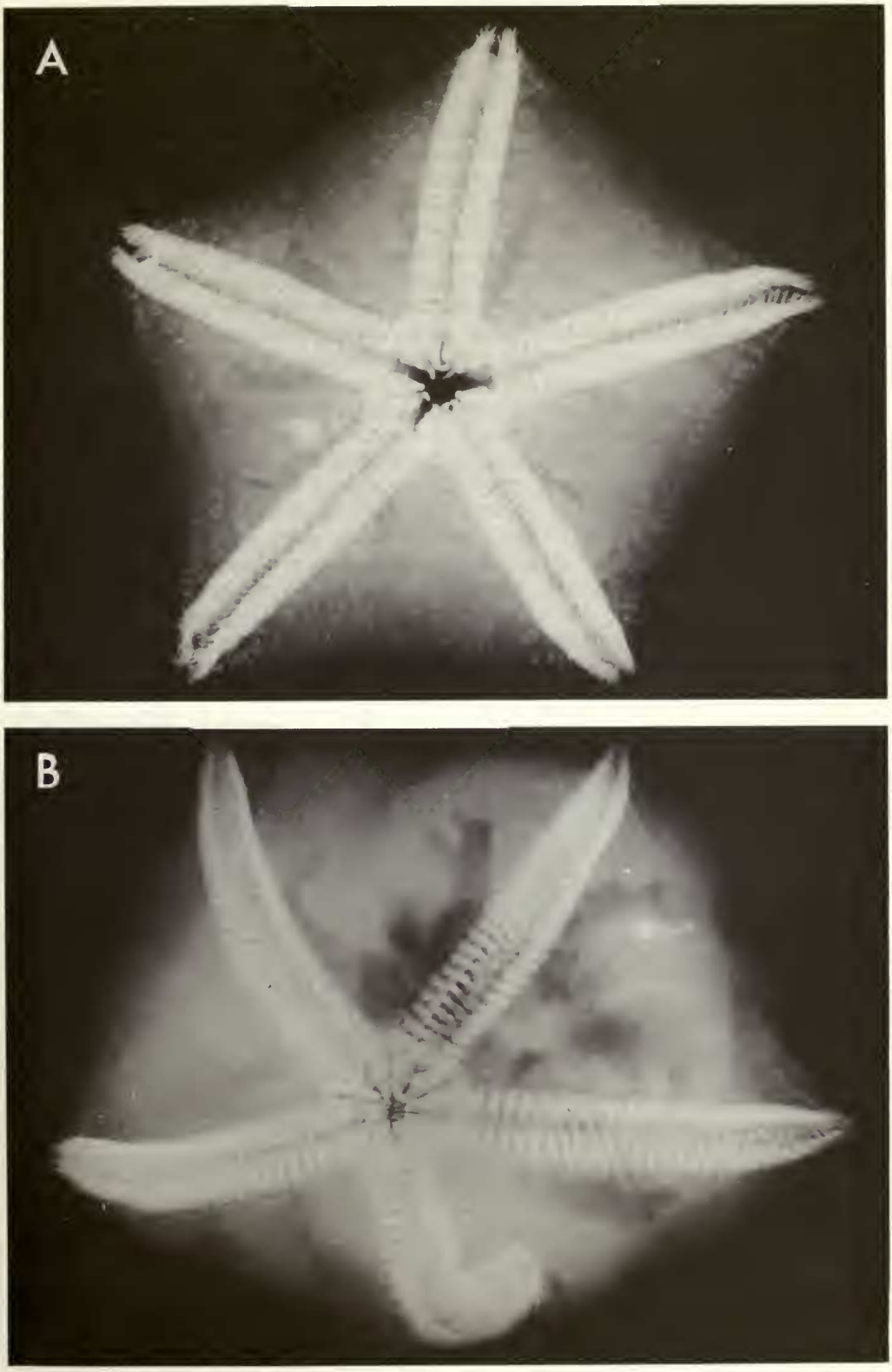

Fig. 13 X-rays of *Poraniomorpha* (*Culcitopsis*) *borealis* (Süssbach & Breckner): A, IOS st. 9752, Porcupine Seabight, R 40 mm; B, 1966.1.13.45, SE of Wyville Thomson Ridge, R. *c.* 47 mm. × 1½.

pentagonal outline, R/r < 1·5/1, are more or less high and cushionlike with the body wall thickened and agree with Süssbach & Breckner's holotype of *C. borealis*, taken NE of the Shetlands in 134–215 metres. The papulae are in close clusters, the upper surface otherwise appearing fairly smooth superficially but studded with numerous embedded fine spinules visible under magnification, the ventral surface somewhat pustular and the adambulacral spines heavily sheathed. Most of these characters are at variance with 'typical' *Poraniomorpha hispida* where the body is flattened though thick and the superficial armament is distinct and almost continuous, covered over with only thin skin.

X-rays of six of the *borealis*-like specimens ranging in size from R 19–72 mm are shown in Figs 12 and 13. As would be expected, the maximum calcification of the skeleton appears in the smallest where the interbrachial septa are partly calcified. However, even here many of the marginals and actinals (or abactinals) showing in the interradii have a fairly large central cavity and the body shape (Fig. 10C) is markedly inflated, much as in Greig's specimen of similar size (1927: 132–133, figs 3–5) from *Michael Sars* st. 32 (W of Kristiansund, Norway, 400 metres, upon which (rather than his larger ones) I suspect Grieg based his observation that 'the skeleton of the disc is well developed and agrees completely with that of *Poraniomorpha hispida'* though he notes that the surface armament is hidden in the thick skin. Although the rate of calcite resorption varies to some extent as shown in the X-rays (compare Figs 12C & 13 A, B), at R > 40 mm only vestigial outlines of most plates are evident, at best. This compares with a flattened Trondheim specimen of *P. hispida* (Figs 9A, B, 10A, 14) with R *c.* 32 mm in which the abactinal and actinal plates and interbrachial septa appear well calcified and the marginals solid and blocklike. Even in a specimen of *hispida* with R > 50 mm, from the Skagerrak in 660 metres, X-ray kindly sent by Dr Madsen, the skeletal development still appears much the same except that the interradial plates of one of the marginal series are reduced and hollowed to a similar extent as the corresponding plates of the *borealis* with R only 19 mm (Fig. 12A). Clearly there should be considerable similarity in the skeletons of juvenile *borealis* and *hispida*, the main skeletal differences

Fig. 14 X-ray of *Poraniomorpha* (*Poraniomorpha*) *hispida* (M. Sars) (as in 9A, B). × 1½.

being in the timing and extent of resorption. However, the resultant morphological difference in well-grown specimens is so marked (compare also the side views shown in Fig. 9B, E) that I find it impossible to believe there is insufficient genetic difference to justify a specific distinction for *borealis,* as well as a subgeneric one for *Culcitopsis* within the genus *Poraniomorpha.* My conclusion that *borealis* is more than just a form of *hispida* is supported by a notable enlargement and distal inclination of a single pair of suboral spines on each jaw of most specimens of *borealis* (see Fig. 11A), suggesting a modification in feeding habits (perhaps approaching that of *Odontaster* which has similar projecting but hyaline-tipped oral spines used for rasping on sponges). A similar modification, but of the apical pair of oral spines, is shared by *Poraniomorpha bidens* Mortensen, 1932: 9–12 from Greenland (recently taken also in the cold area of the Faeroe Channel NE of the Wyville Thomson Ridge). *P. bidens* has a furlike coating of very fine superficial spinules of papillae clearly visible through the thin skin, as in *P. hispida,* but a general body form with tapering pointed rays, as in the other arctic species, *P. tumida* (Stuxberg) where the superficial armament is much coarser, almost granuliform. Additionally, the colour in life of *borealis* appears to be generally much paler than that of *hispida,* the darkest cited being pale orange above; it is more often yellow or pale yellow, white below, whereas *hispida* is said to be: rose red above, orange below; dark violet-red above with white papulae, reddish-white below, or pale reddish-yellow all over.

As mentioned previously (p. 34), intermediates exist in northern Norway between the polymorphic *hispida* and *tumida* where the two taxa overlap. Clearly the taxonomy of the entire genus *Poraniomorpha* needs to be reviewed, not just the Atlantic members within the scope of the present study.

It should be noted that in addition to the natural differences correlated with the skeletal development, decalcified specimens can be drastically modified in appearance by changes in preservation. For instance, the large specimen, R 72 mm (Fig. 12D) from the Lofoten Is in the British Museum collection, thought to be *P. (C.) borealis* is badly flattened with the upper side crinkled and the whole body wall excessively contracted so that the superficial spinules are brought together in an almost continuous coating, as is usual in *Poraniomorpha hispida,* the identification it had prior to being X-rayed. The extent of shrinkage possible in these poraniids is shown by the holotype of *Sphaeriaster berthae* (Dons, 1938: 163–164), from N of the Lofoten Is, which had R 90–115 mm in life but was only 77–80 mm after preservation in spirit. Change in body shape may also be drastic, as shown by *Spoladaster veneris* (Perrier), from St. Paul's I, southern Indian Ocean where live specimens may be markedly stellate but preserved ones become pentagonal—see A.M.C., 1976, pl. 6 and pl. 3, fig. 2. Madsen and I have no doubt that *S. berthae* is synonymous with *borealis* so that **Sphaeriaster** itself is a synonym of *Poraniomorpha.* Dons's second nominal species, *S. bjoerlykkei,* (1938: 165–168) type locality N of the Shetlands in 300–350 metres, R/r 87/47 = 1·7/1 so fairly stellate, shows a high density of superficial spinules as in our Lofoten Is specimen just mentioned. A new X-ray sent by Madsen shows very faint outlines of plates, much as in large *borealis*, but he thinks that it is more likely to be decalcified *P. tumida*; Dons described multiple furrow and subambulacral spines, more than usual in *borealis.*

Another taxon with a very reduced skeleton in larger specimens is **Spoladaster** Fisher. In 1976 (in Clark & Courtman-Stock: 73) I suggested that *Tylaster meridionalis* Mortensen, 1933: 249–250, from the same area W of South Africa, based on a specimen with R only 28 mm, is probably a synonym of *S. brachyactis* (H. L. Clark, 1923: 293–294), of which R is 40–80 mm in the few specimens recorded. Studies now on the growth changes and variation of *P. (C.) borealis* confirm me in this view. It is noteworthy that no better-calcified Poraniomorphas have been collected in south african waters. *S. brachyactis* shows some development of macroscopic inferomarginal and actinal spines, such as are found in greater numbers in *Tylaster willei* Danielssen & Koren, 1881: 186, from the northern Norwegian Sea (see Danielssen & Koren, 1884: 64–67). This species too has the underlying skeleton very reduced. These taxa illustrate the ability of poraniids to utilize coarse armament even though this is, at best, articulated only to rudiments of skeletal plates in the thickened body

wall. **Tylaster** and the other arctic taxa mentioned come within the range of the series 'Marine Invertebrates of Scandinavia', the asteroid part of which is in preparation by Madsen. Hopefully he will be able to clarify the relationships of these if more material is available.

There is yet one more conspicuous example of skeletal reduction in poraniids, exemplified by **Pseudoporania** Dons. Again I am indebted to Madsen for an X-ray, of the holotype of *P. stormi* Dons, 1936: 17–20, from Trondheim fjord in 300 metres, R 83–96 mm. This shows that the actinal and marginal plates have contracted down into very small, widely separated rods or partially hollow nodules of calcite, the more interradial inferomarginals being apparently reduced to a rudiment of their abradial, possibly also adradial ends. This is just the progression I would expect from the condition found in six much smaller specimens, R 19–40 mm, one from the Porcupine Seabight, the others from around the Wyville Thomson Ridge, S of the Faeroes, in depths of 360 (?183)–770 (?927) metres. These too have a smooth surface above and below, apart from well-marked actinal grooving. Sectioning shows the lateral body wall to be extremely thick (Fig. 5B) and X-rays show no signs of inferomarginal spines, even on the distal plates in the smallest (Fig. 16A, B), the ambitus being rounded. The body form is flattened and pentagonal whereas Don's specimen has short tapering rays. The papulae are relatively sparse and scattered. The adambulacral plates are armed with single furrow and subambulacral spines (the sheath of the latter continuous with the thickened ventral body wall), which appeared to provide a distinction from *stormi* but Madsen informs me that it too has single spines, Dons' description of 2+2 being incorrect. The smallest specimen has the marginals blocklike except for the interradial inferomarginals which project abradially. The sections and X-rays show progressive attenuation of the plates with division of the interradial inferomarginals into two small end pieces, ad- and abradial, by loss of the middle part. This is very different from the resorption shown by *Poraniomorpha (C.) borealis*, which is almost entirely from the inside, the plates being reduced to hollow, usually rectangular or ovate, shells. The complete absence of any superficial spinules and the small number of adambulacral spines, with only single furrow spines, agrees more closely with **Porania** than any other genus of the family, though the great thickening of the body wall and the absence of a distinct ventrolateral angle emphasized by a horizontal fringe of individually sheathed inferomarginal spines results in a very different appearance.

In 1983 (*in* Gage et al.: 281) I noted that a specimen of *Porania pulvillus* (O. F. Müller, 1776: 234) from the Rockall Bank in 148 metres with R 55 mm has the inferomarginal spines drastically reduced from the usual 3–5 on each plate to only 1 or 2 on some of the more interradial plates and none on the distal plates. Nevertheless, the remaining spines are individually sheathed and projecting from the ambitus and the usual ventrolateral angle is still distinct, the body wall not being markedly thickened. An X-ray of this specimen (Fig. 18B) shows that a few of the interradial inferomarginal plates are slightly compressed, recalling those of the smallest specimen of *stormi* (Fig. 16A), though the modification is much less. Madsen (pers. comm.) has found occasional specimens of *P. pulvillus* from Norway with the inferomarginal spines more or less reduced but the skeleton otherwise well developed. Additionally he has sent X-rays of two other specimens, R probably 25–30 mm, with the interradial marginals much reduced, some divided into two parts and the body wall obviously much thickened. Although he finds these akin to *Pseudoporania stormi,* he considers this to be a synonym of *Porania pulvillus.* One (from S of Iceland, *Thor* st. 166) appears to have nearly all the marginals narrowed down and completely lacking spines, much as in the Porcupine Seabight specimen (Fig. 16B) but the other (Tromsø Museum, probably from N Norway) has about 3 inferomarginal plates each side of the very reduced interradial plates in each interbrachial arc with a rhombic abradial part bearing 1, rarely 2, large spatulate spines.

In face of such intermediate specimens, there can be little doubt that *Pseudoporania* should be referred to the synonymy of *Porania,* in a comparable way to *Culcitopsis* and *Poraniomorpha.* However, the general form of adults of the several *Porania* species, with a distinct ventrolateral angle and the body wall no more than moderately thickened is so

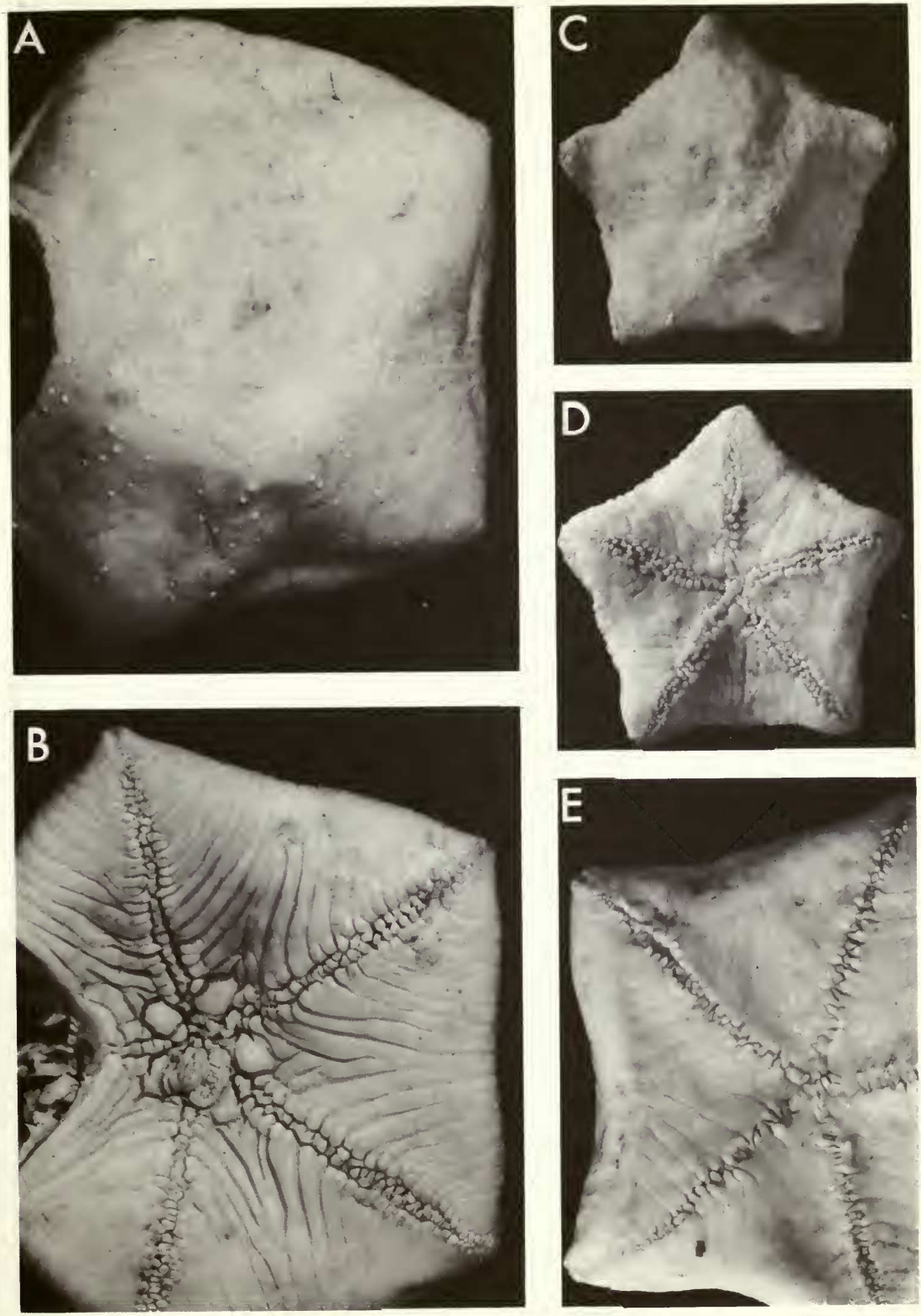

Fig. 15 *Porania* (*Pseudoporania*) *stormi* (Dons): A, B, (as in 5B), dorsal and ventral views; C, D. Royal Scottish Museum, *Walter Herwig* st. 848, S of Faeroe Is, R 19 mm, dorsal and ventral views; E, IOS st. 50601, Porcupine Seabight, R 35 mm. All wet, $\times 1\frac{1}{2}$.

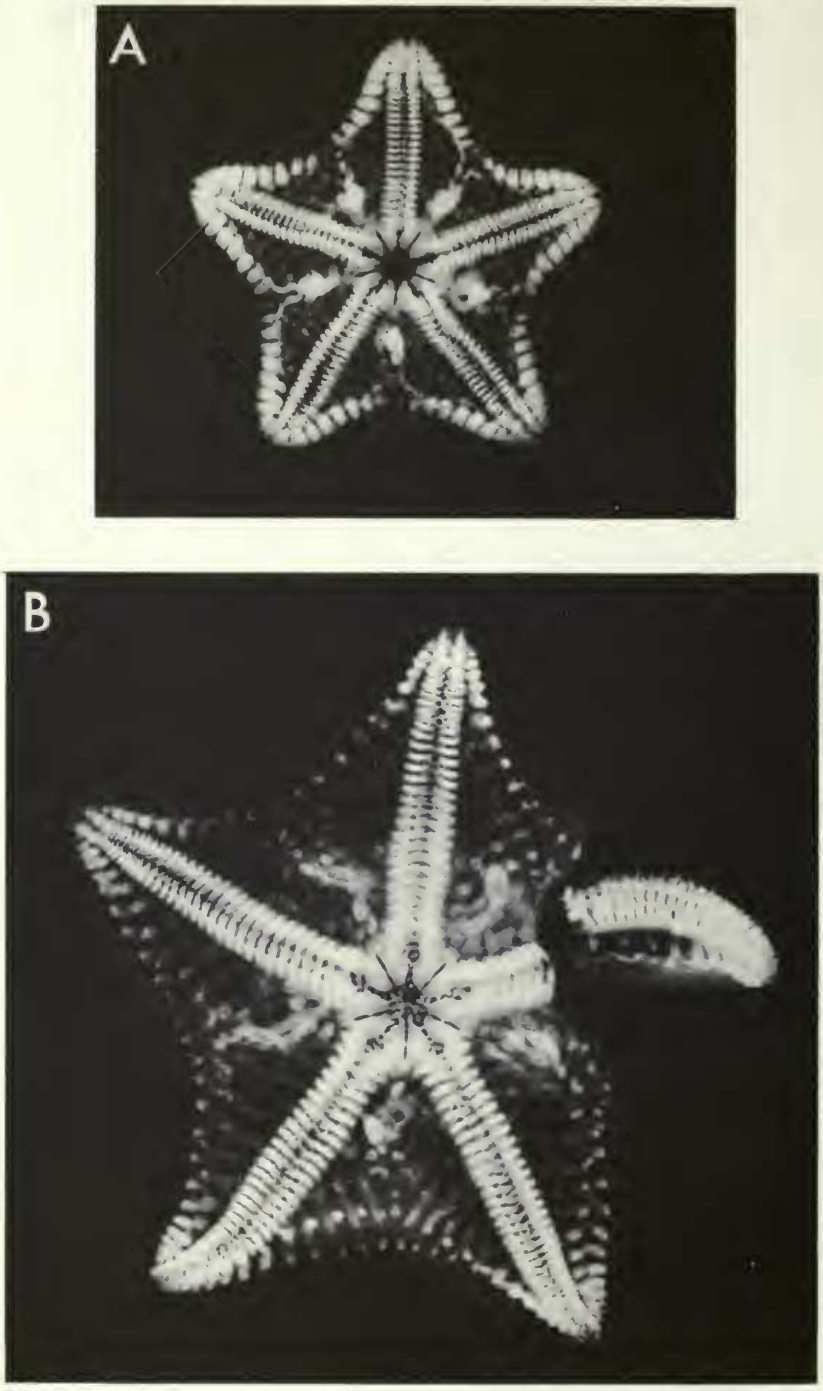

Fig. 16 X-rays of *Porania* (*Pseudoporania*) *stormi* (Dons): A (as in 15B, C); B (as in 15E). × 1½.

consistent that here again I believe a subgeneric distinction is justified, in spite of Madsen's opinion to the contrary. It seems likely that *P. stormi* is zoogeographically isolated from *pulvillus*. The present records indicate that *pulvillus* alone is found on the shelf around the British Isles and in southern Norway N to about Trondheim fjord, to a minimum depth of

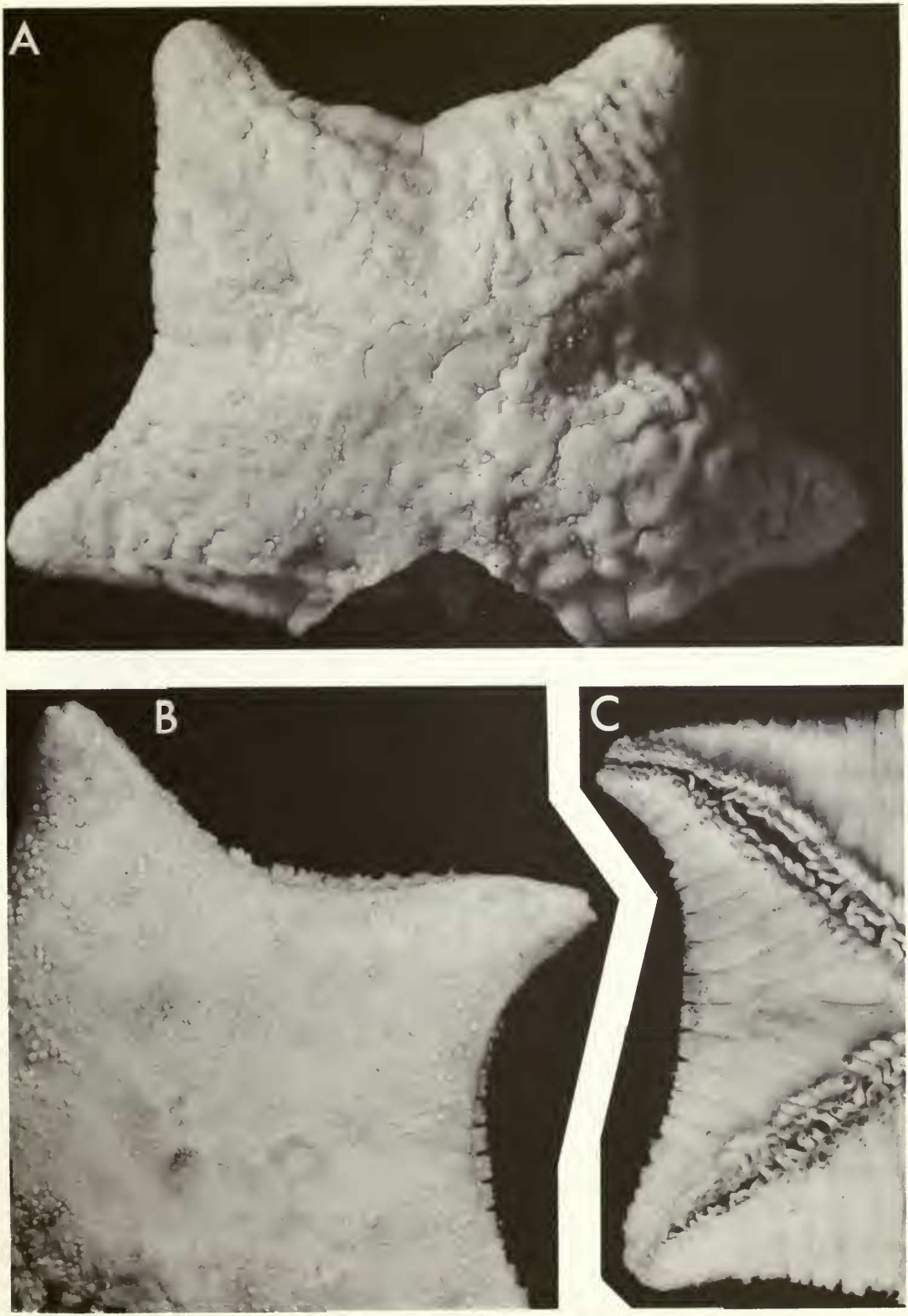

Fig. 17 *Porania (Porania) pulvillus* (O. F. Müller): A (as in 5C); B, C, 1950.11.3. 1, Porcupine Bank, R 55 mm, dorsal and part ventral views. Both wet, $\times 1\frac{1}{2}$.

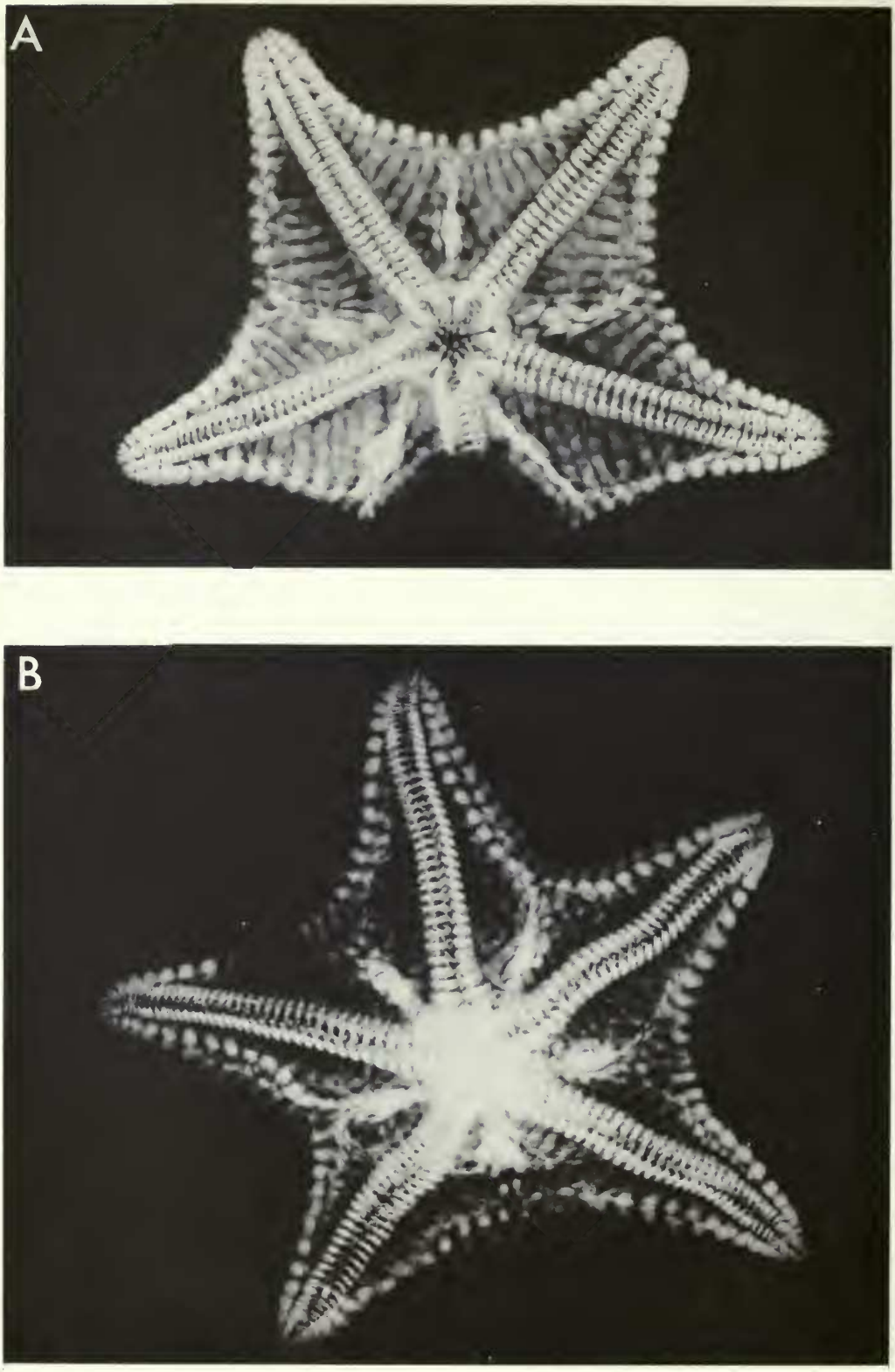

Fig. 18 X-rays of *Porania* (*Porania*) *pulvillus* (O. F. Müller): A (as in 5C); B, 1981.3.24.28, Rockall Bank, R 55 mm (the inferomarginal spines only show in one interradius though in fact present in the others; a section of one arm removed). × 1½.

5 metres (a new record from Lunna, Shetland Is where it was collected by a diver) and a maximum of *c.* 250 metres, whereas *P. stormi* is an upper bathyal species limited to more remote areas, from S of Iceland to the continental slope W of the British Isles and possibly from N Norway.

However, there is a much closer morphological resemblance between *Porania pulvillus* and the american *P. insignis* Verrill, 1895: 138–139. The former is consistently relatively thin-walled with a well-marked ventrolateral angle. Although the available material suggests that the abactinal skeleton may be more open in the american taxon, the main difference is that some adults retain a few actinal spines whereas these are almost invariably lost at an early stage in *P. pulvillus.* Madsen (pers. comm.) has independently reached the same conclusion.

To provide a summary of the main diagnostic characters used in identification of poraniids, a tabular key to the genera and subgenera now accepted is given here (Table 2).

Table 2 Tabular key to the genera of Poraniidae. Alternate columns in lower case.

	1	2	3	4	5	6	7
Poraniopsis	W	s(i)	C–O	r	SD	q+	T
Porania (*Porania*)	W(R)	n,s(i)	O	a	SC	q+/–	T
Porania (*Pseudoporania*)	R	n	O	r	L	q–	T
Tylaster	R	i	?	r	S*(D)	q+	T
Spoladaster	R	i	O(C)	r	SD	q,p(+)	T
Chondraster	R	n	O	a(r)	H	q–[+]	M
Poraniomorpha (*Culcitopsis*)	R	i	C	r	L[M]	p–	M(T)
Poraniomorpha (*Poraniomorpha*)	W	f	C(S)	r	M	s+/–	M(T)
Marginaster	[W]	[s]	[S]	[a]	[SC]	[q–]	[T]

Note: Square brackets indicate occurrence in small specimens, as throughout in *Marginaster;* round brackets show the condition in occasional specimens or a modified form. *In *Tylaster willei* the inferomarginal spines are evidently in triangular groups of three, not a horizontal line.

1. Abactinal skeleton:
   W–well developed
   R–more or less reduced by resorption, especially in large specimens, R > 50 mm
2. Superficial dorsal body wall:
   f–with very fine continuous or clustered spinules, tubercles or papillae, not necessarily articulated to the underlying plates
   i–with fine isolated spinules, not articulated to the plates
   n–naked and smooth, sometimes with surface spicules so dense as to show a pale colour when dried
   s–with spaced relatively large spines mounted on the larger plates or vestiges of plates
3. Papulae:
   C–clustered
   O–in open groups, short arcs or evenly spaced over wide areas
   S–single
4. Shape of margin:
   a–more or less distinctly angular ventrolaterally, corresponding to the horizontally projecting inferomarginals
   r–rounded, the inferomarginals hardly, if at all, projecting or else both series of plates reduced
5. Inferomarginal armament:
   H–hidden in live or well-preserved specimens, the few large spines wholly within the much thickened body wall
   L–lacking altogether
   M–of multiple spinelets clustered along the ventrolateral convexity
   S–of up to 5 large spines in a horizontal row, at least their tips projecting, forming either a continuous fringe (C) or a discontinuous grouped series (D)
6. Appearance of actinal areas (apart from the ciliated grooves between the furrows and margins):
   p–pustular
   q–quite smooth (apart from any macroscopic armament)
   s–with fine superficial spinules, usually slightly spaced
   +/– with or without enlarged spinelets or spines in series parallel to the inferomarginals
7. Adambulacral armament:
   T–arranged normally in one series transverse to the furrow, usually 2 or 3 spines
   M–with multiple furrow spines on most plates, subambulacral spines variously arranged, paired, in an oblique but nearly longitudinal series within a common sheath, or transversely

Nomenclature

The classification of the Poraniidae has been complicated not only by the thick skin obscuring the usual diagnostic characters afforded by the skeleton but also by failure to allow for ontogenetic changes and an unwise propensity of certain early workers to give new names to juvenile or small specimens. Consequently, the names of certain species-group taxa are threatened by the possibility that they will be proved to be synonymous or homonymous with prior nominal species, as follows:

Poraniomorpha (Culcitopsis) borealis (Süssbach & Breckner, 1911) is threatened by two possibilities, firstly:

Asterina borealis Verrill, 1878 (holotype extant in the Peabody Museum, Yale, R 12 mm), long synonymized with *P. hispida,* may prove to be consubspecific with *P. (Poraniomorpha) hispida rosea* Danielssen & Koren, 1881, which it antedates. In this eventuality and if the subspecies now proposed is accepted, then *borealis* Verrill would be a senior species-group homonym within the genus *Poraniomorpha.*

Secondly:

Marginaster pentagonus Perrier, 1882 (holotype extant in the Paris Museum, R only 3 mm) may prove to be a senior synonym. The name *pentagonus* has only been mentioned as a possible synonym since Perrier, 1894.

Porania pulvillus insignis Verrill, 1895 is threatened by:

Asterina pygmaea Verrill, 1878 (holotype extant in the Peabody Museum, R only 5 mm), which may prove to be a senior synonym. The name *pygmaea* has been unused since referred to *Poranisca* by Verrill, 1914.

Porania antarctica Smith, 1876 is threatened by:

Astrogonium fonki Philippi, 1858, which Madsen (1956) has little doubt was based on specimens conspecific with *P. antarctica magellanica* Studer, 1876 but which he assumed are no longer extant in any chilean collection since they were not mentioned in Meissner's note on Philippi's asteroids of 1898. The name *fonki* has been unused since 1858 but *P. antarctica* is widely utilized.

Summary of taxonomic confirmations or changes

Poraniella Verrill, 1914, referred to the family Asteropseidae from Poraniidae.

Poraniopsis Perrier, 1891, referred to the family Poraniidae from Echinasteridae.

Poranisca Verrill, 1914, with type species *P. lepidus* Verrill, 1914, synonyms of *Marginaster* Perrier, 1881 and *M. pectinatus* Perrier, 1881.

Chondraster Verrill, 1895, confirmed as of generic rank, distinct from *Porania* Gray, 1840.

Poraniomorpha rosea Danielssen & Koren, 1881, treated as a subspecies rather than a form or variety of *P. hispida* (M. Sars, 1872).

Culcitopsis Verrill, 1914, type species *Culcita borealis* Süssbach & Breckner, 1911, treated as subgenus of *Poraniomorpha* Danielssen & Koren, 1881.

Culcitopsis borealis (Süssbach & Breckner), treated as a separate species rather than a form of *Poraniomorpha hispida* (M. Sars).

Sphaeriaster Dons, 1939, type species *Sphaeraster berthae* Dons, 1938, synonyms of *Poraniomorpha (Culcitopsis)* Verrill and *P. (C.) borealis* (Süssbach & Breckner).

Tylaster meridionalis Mortensen, 1933, confirmed as a synonym of *Spoladaster brachyactis* (H. L. Clark, 1923).

Pseudoporania Dons, 1936, type species *P. stormi* Dons, 1936, a subgenus of *Porania* Gray.

Porania insignis Verrill, 1895, reduced to a subspecies of *P. pulvillus* (O. F. Müller).

Taxa the affinities of which need further investigation:

Asterina borealis Verrill, 1878 and *Porania spinulosa* Verrill, 1880, as infraspecific taxa within, rather than pure synonyms of, *Poraniomorpha hispida* (M. Sars).

Marginaster austerus Verrill, 1899, in relation to *M. pectinatus* Perrier.

Marginaster fimbriatus Sladen, 1889, in relation to *Chondraster grandis* (Verrill, 1878).

Marginaster pentagonus Perrier, 1882, in relation to *Poraniomorpha hispida borealis* (Süssbach & Breckner).

Sphaeriaster bjoerlykkei (Dons, 1938), in relation to *Poraniomorpha hispida borealis* (Süssbach & Breckner) *and P. tumida* (Stuxberg, 1878).

Tylaster Danielssen & Koren, 1881, with type species *T. willei* Danielssen & Koren, 1881, in relation to *Chondraster* Verrill, 1895 and *Porania* Gray.

Spoladaster Fisher, 1940, with type species *Cryaster brachyactis* H. L. Clark, 1923, in relation to *Poraniomorpha* Danielssen & Koren.

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References

Bell, F. J. 1893. *Catalogue of the british echinoderms in the British Museum (Natural History).* xvii+202 pp. London: Trustees of the British Museum.

Blake, D. B. 1980. On the affinities of three small sea-star families. *Journal of Natural History.* **14:** 163–182.

—— 1981. A re-assessment of the sea-star orders Valvatida and Spinulosida. *Journal of Natural History.* **15:** 375–394.

Cherbonnier, G. & Sibuet, M. 1973. Résultats scientifiques de la campagne Noratlante: Astéroides et Ophiurides. *Bulletin du Muséum National d'Histoire Naturelle, Paris.* (Zoologie) No. 76 [1972]: 1333–1394.

Clark, A. M. 1976. Asterozoa from Amsterdam and St Paul Islands, southern Indian Ocean. *Bulletin of the British Museum (Natural History)* (Zoology) **30:** 247–261.

Clark, A. M. & Courtman-Stock, J. 1976. *The echinoderms of southern Africa.* 277 pp. London: Publications of the British Museum (Natural History) No. 776.

Clark, H. L. 1923. The echinoderm fauna of South Africa. *Annals of the South African Museum.* **13:** 221–435.

Danielssen, D. C. & Koren, T. 1881. Fra den norske Nordhavs-expedition: Echinodermer. *Nyt Magazin for Naturvidenskaberne.* **26:** 177–195.

—— 1884. Asteroidea. *Den norske Nordhavs-expedition, 1876–1878.* 119 pp. Christiania.

Djakonov, A. M. 1946. [Individual and age variability in some groups of echinoderms.] *Trudy Zoologicheskogo Instituta, Leningrad* **8:** 145–193.

—— 1950. [Sea stars of U.S.S.R. seas.] *Opredeliteli po Faune SSSR.* no. 34: 1–199. [English translation: Jerusalem. 1968. 183 pp.]

Dons, C. 1936. Zoologische Notizen. 26. *Pseudoporania stormi* n. gen., n. sp. *Kongelige Norske Videnskabernes Selskabs Forhandlinger.* **8:** 17–20.

—— 1938. Zoologische Notizen. 35, 36. *Sphaeraster Berthae* n. gen., n. sp. *Sphaeraster Björlykkei* n. sp. *Kongelige Norske Videnskabernes Selskabs Forhandlinger.* **10:** 161–168.

—— 1939. Zoologische Notizen. 37. Die Asteriden Gattung *Spaeriaster,* nomen novum. *Kongelige Norske Videnskabernes Selskabs Forhandlinger.* **11:** 37.

Downey, M. E. 1973. Starfishes from the Caribbean and the Gulf of Mexico. *Smithsonian Contributions to Zoology* No. 126: 1–158.

Farran, G. P. 1913. The deep-water Asteroidea, Ophiuroidea and Echinoidea of the west coast of Ireland. *Scientific Investigations. Fisheries Branch, Department of Agriculture for Ireland.* **6:** 1–66.

Fisher, W. K. 1908. Necessary changes in the nomenclature of starfishes. *Smithsonian Miscellaneous Collections.* **52:** 87–93.

—— 1911. Asteroidea of the North Pacific and adjacent waters. 1. *Bulletin of the United States National Museum.* **76**(1): vi+419 pp.
—— 1940. Asteroidea. *Discovery Reports.* **20:** 69–306.
Gage, J. D., Pearson, M., Clark, A. M., Paterson, G. L. J. & Tyler, P. A. 1983. Echinoderms of the Rockall Trough and adjacent areas. 1. *Bulletin of the British Museum (Natural History)* (Zoology) **45:** 263–308.
Gallo, V. R. 1937. Sur le genre "Culcitopsis" Verrill (Astéroides). *Compte Rendu XII^e Congrès International Zoologique. Lisbon, 1935:* 1664–1667.
Gasco, F. 1876. Descrizione di alcune Echinodermi nuovi o per la prima volta trovato nel Mediterraneo. *Rendiconti dell'Accademia delle Scienze Fisiche e Matematiche. Napoli.* **15**(2): 9–11.
Gray, J. E. 1840. A synopsis of the genera and species of the class Hypostoma (*Asterias,* Linn.). *Annals and Magazine of Natural History* **6:** 175–184; 275–290.
Grieg, J. A. 1907. Echinodermen von dem norwegischen Fischereidampfer "Michael Sars" in den Jahren 1900–1903 gesammelt. Asteroidea. *Bergens Museum Arbog* **1906**(13): 1–87.
—— 1927. Echinoderms from the west coast of Norway. *Nyt Magazin for Naturvidenskaberne.* **65:** 127–136.
Hotchkiss, F. H. C. & Clark, A. M. 1976. Restriction of the family Poraniidae, sensu Spencer & Wright. *Bulletin of the British Museum (Natural History).* (Zoology) **30:** 263–268.
Koehler, R. 1921. Echinodermes. *Faune de France* **1:** 1–210.
—— 1924. *Les Echinodermes des Mers d'Europe.* 1. 360 pp. Paris: Librarie Octave Doin.
Leipoldt, F. 1895. Asteroidea der "Vettor-Pisani" Expedition (1882–1885). *Zeitschrift für Wissenschaftliche Zoologie.* **59:** 545–654.
Ludwig, H. 1897. Die Seesterne des Mittelmeeres. *Fauna und Flora des Golfes von Neapel.* **24:** 1–491.
Madsen, F. J. 1956. Reports of the Lund University Chile Expedition, 1948–49. 24. Asteroidea. *Acta Universitatis Lundensis.* Andra Afd. N.S. **52**(2): 1–53.
—— 1959. A new North Atlantic sea-star, *Chondraster hermanni* n. sp., with remarks on related forms. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening.* **121:** 153–160.
Meissner, M. 1898. Ueber chilenische Seesterne. *Zoologischer Anzeiger.* **21:** 394, 395.
Mortensen, T. 1912. Report on the echinoderms collected by the Danmark-Expedition at North-East Greenland. *Meddelelser om Grønland.* **45:** 237–302.
—— 1927. *Handbook of Echinoderms of the British Isles.* ix+471 pp. London: Oxford University Press.
—— 1932. Echinoderms of the Godthaab Expedition of 1928. *Meddelelser om Grønland.* **79:** 1–62.
—— 1933. Echinoderms of South Africa (Asteroidea and Ophiuroidea). *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening.* **93:** 215–400.
Müller, O. F. 1776. *Zoologiae danicae prodromus.* xxxii+282 pp. Havniae.
Östergren, H. 1904. Ueber die arktischen Seesterne. *Zoologischer Anzeiger.* **27:** 615–616.
Perrier, E. 1881. Description sommaire des espèces nouvelles d'Astéries. *Bulletin of the Museum of comparative Zoology, Harvard.* **9:** 1–31.
—— 1882. *In*: Milne Edwards. Rapports sur les travaux de la Commission chargée par M. le ministre de l'Instruction publique d'étudier la faune sous-marine dans le grandes profundeurs de la Méditerranée et de l'Atlantique. *Archives des Missions Scientifiques et Litteraires. Paris.* (3)**9:** 46–49.
—— 1884. Mémoire sur les étoiles de mer recueillies dans la Mer des Antilles et la Golfe de Mexique. *Nouvelle Archives du Muséum d'Histoire Naturelle, Paris* (2)**6:** 127–276.
—— 1891. Echinodermes. 1. Stellérides. *Mission Scientifique du Cap Horn. 1882–1883.* **6:** Zoologie. (3) 198 pp. Paris.
—— 1893. *Traité de Zoologie.* 1 & 2. 864 pp. Paris: Librairie F. Savy.
—— 1894. Stellérides. *Expeditions scientifiques du Travailleur et du Talisman.* 431. pp. Paris.
Philippi, R. A. 1858. Beschreibung einiger neuer Seesterne aus dem Meere von Chiloe. *Archiv für Naturgeschichte.* **24:** 264.
Sars, M. 1872. Tillaeg. In: Sars, G. O. Nye Echinodermer fra den Norske Kyst. *Forhandlinger i Videnskabsselskabet i Kristiania.* **1871:** 27–31.
—— 1877. New echinoderms. In: Koren & Danielssen [Eds] *Fauna littoralis Norvegiae.* **3:** 49–75. Bergen.
Sladen, W. P. 1889. Asteroidea. *Report of the scientific results of the voyage of H.M.S. Challenger, 1873–76.* Zoology, **30:** 1–935.
Spencer, W. K. & Wright, C. W. 1966. Asterozoans. In: Moore, R. C. [Ed.] *Treatise on Invertebrate Paleontology.* U. Echinodermata **3**(1): 4–107. Geological Society of America Inc.: University of Kansas Press.

Stuxberg, A. 1878. Echinodermer fran Novaja Zemljashaf samlade under Nordenskioldska Expeditionerna, 1875 och 1876. *Ofversigt af Kongl, Vetenskaps–Akademiens Förhandlingar. Stockholm.* **1878**(3): 27–40.

Süssbach, S. & Breckner, A. 1911. Die Seeigel, Seesterne und Schlangensterne der Nord- und Ostsee. *Wissenschaftliche Meeresuntersuchungen der Kommission zur Wissenschaften Untersuchung der Deutschen Meere.* Abteilung Kiel. N.S. **12:** 167–300.

Tortonese, E. 1965. Echinodermata. *Fauna d'Italia.* **6:** xv+422. Bologna: Edizioni Calderini.

Verrill, A. E. 1878. Notice of recent additions to the marine fauna of the eastern coast of North America. 1, 2. *American Journal of Science.* (3) **16:** 207–215; 371–378.

—— 1880*a*. Notice of recent additions to the marine Invertebrata of the northeastern coast of America. *Proceedings of the United States National Museum.* **2:** 165–205.

—— 1880*b*. Notice of the remarkable marine fauna occupying the outer banks off the southern coast of New England. *American Journal of Science.* (3)**20:** 390–403.

—— 1885. Results of the explorations made by the steamer "Albatross" off the northern coast of the United States in 1883. *Report United States Commissioner of Fisheries.* **1883:** 503–543.

—— 1895. Distribution of the echinoderms of north-eastern America. *American Journal of Science.* **49:** 127–141; 199–212.

—— 1899. Revision of certain genera and species of starfishes with descriptions of new forms. *Transactions of the Connecticut Academy of Arts and Sciences.* **10:** 145–234.

—— 1914. Revision of some genera and species of starfishes. *Annals and Magazine of Natural History.* **14:** 13–22.

—— 1915. Report on the starfishes of the West Indies, Florida and Brazil. *Bulletin from the Laboratories of Natural History of the State University of Iowa.* **7**(1): 1–232.